SPONGOPHYLLIDAE FROM THE DEVONIAN GARRA FORMATION, NEW SOUTH WALES

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ABSTRACT. The structure of rugosans belonging to the family Spongophyllidae Edwards and Haime 1873 (here taken to include the Family Ptenophyllidae Wedekind 1923) is discussed in detail. Representatives of the Family occurring in the Emsian (or possibly early Eifelian) Garra Formation are revised or described. The Australian species ascribed to *Acanthophylluan* are reviewed, *Pseudochonophyllum* Soshkina is fully revised, and its type (and only) species, *P. pseudohelianthoides* (Sherzer) is shown to occur only in Czechoslovakia and eastern Australia. *Grypophyllum aggregatum* Hill is placed in *Lyrielasma* Hill. *Australophyllum* Stumm is discussed and its species are reviewed. Several of the eastern Australian Devonian faunas, previously thought to range from Coblenzian to late Eifelian, are considered to be probably Emsian.

New species described are: Acanthophyllum (Acanthophyllum) aeneae, A. (Neostringophyllum) implicatum, A. (N.) turni, A. (Grypophyllum) jenkinsi, Lyrielasma? micrum, Australophyllum bilaterale.

In this paper are described those species of corals, occurring in the Emsian? Garra Formation of New South Wales, which comprise the acanthophyllid and spongophyllid groups. For reasons outlined below, these are for the present at least combined into the Family Spongophyllidae.

The Garra Formation has been described in a previous paper on the disphyllids and phacellophyllids (Strusz 1965b), and in a purely stratigraphic Note (Strusz 1965a). Further references, both geological and palaeontological, may be found therein. An additional reference of some interest in the correlation of this formation is Philip and Pedder (1964).

Abbreviations. The following abbreviations (fully explained in Strusz 1965 b, p. 522) are used herein:

- Dc Corallite diameter
- Dt Tabularium diameter
- R Corallite radius
- Ts Tabularial spacing (astraeoid, etc., coralla)
- n Number of septa
- L₁ Length of major septa
- L_2 Length of minor septa

The repositories of type and other specimens are indicated by the following prefixes to their catalogue numbers:

- AM Thin section numbers, Australian Museum, Sydney, N.S.W.
- AM F Fossil numbers, Australian Museum
- GSQ Geological Survey of Queensland
- GSV Geological Survey of Victoria
- NM National Museum, Melbourne, Victoria
- SU University of Sydney Palaeontological Collection; Sydney, N.S.W.
- UCT F University College of Townsville Palaeontological Collection; Townsville, Qld.
- UQF University of Queensland Palaeontological Collection; Brisbane, Qld.

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SYSTEMATIC PALAEONTOLOGY

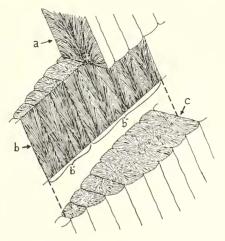
Family SPONGOPHYLLIDAE Dybowski 1873, emend, Pedder 1964

Remarks, Following Pedder (1964, p. 436), and a tentative suggestion by Birenheide (in litt.), I place the Family Ptenophyllidae Wedekind 1923 in synonymy with this family. The thus enlarged family has the following characters:

Septa. The septal structure is rather similar to that of the Disphyllidae. The septa consist of fine trabeculae, in most cases arranged in single radial series, although in some genera there may be more than one series in outer parts of the septa. The trabeculae are arranged either broadly parallel, and inclined upwards and inwards, or in half-fans

within the disseptimentarium, and usually again in the tabularium. This arrangement has been well described by Birenheide (1961).

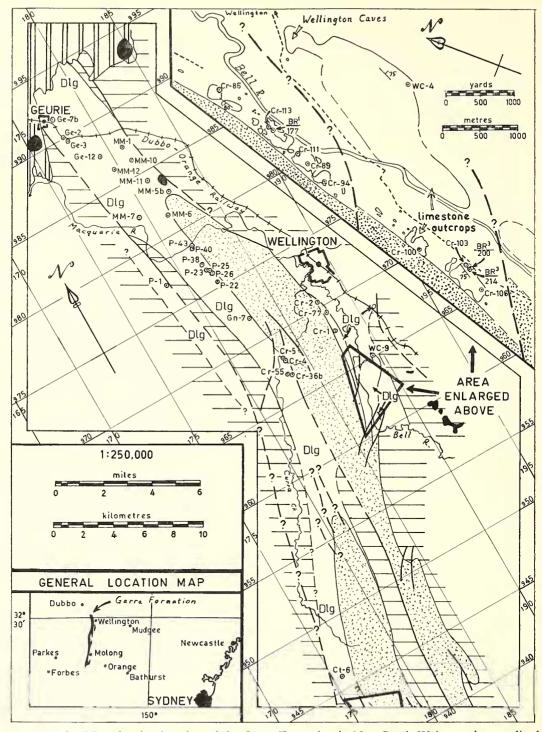
The trabeculae are monacanthine: in crosssection they are round to square in attenuate portions of a septum, becoming oval to rectangular (the long axis perpendicular to the plane of the septum) in dilated portions. Within a trabecula the fibres diverge from the axis, strongly in a tangential direction (i.e. longitudinal, and perpendicular to the plane of the septum), but only weakly in a radial direction (text-fig. 1). In transverse section a septum gives the appearance of a median dark line, from which the fibres diverge at a large angle, apparently without clear trabecular organization. As shown by Birenheide (1961, p. 85) the median dark line represents that region in which the fibres are perpendicular to the section. In tangential longitudinal section the fibres are seen to diverge strongly from the mid-line of the septum. Only in radial longitudinal section may the trabecular arrangement be University of Queensland. a, tangential seen, and even then often not very clearly. In such sections there is also seen a parallel banding perpendicular to the direction of the trabeculae. This is apparently formed partly by periodic variation in emphasized; b", appearance in thin either optical orientation or composition, and partly section; c, transverse section, with traby periodic insertion of additional trabeculae as the trabecular fan expands.



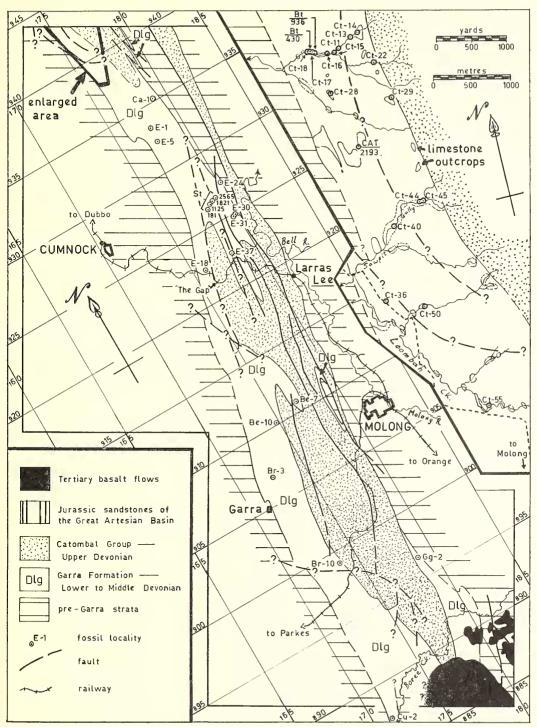
TEXT-FIG. 1. Generalized septal microstructure of the Family Spongophyllidae, approximately \times 50, reconstructed mainly from thin sections of Eifel species of Acanthophyllum in the collection of the longitudinal section along the axis of one trabecula; b, radial longitudinal section along the median plane of the septum; b', boundaries between trabeculae becular boundaries as for b', b''.

In cases where parts of the septa consist of more than a single series of trabeculae, the median dark line is normally absent. The individual trabeculae are round in section, and do not greatly diverge from the direction of the septal plane. Moreover, there is generally no regular arrangement into radial series in such cases. This condition is known peripherally in Dohmophyllum, and over much of the disseptimentarium in Pseudochonophyllum.

There are no carinae (ridges on the side of a septum, formed by the lateral extension of one, or a series of successive, trabeculae at all stages of growth, and so growing in the same direction as the trabeculae). Septal modifications may be of several forms:



TEXT-FIG, 2a. Map showing location of the Garra Formation in New South Wales, and generalized geological map showing positions of fossil localities mentioned in the text.



TEXT-FIG. 2b. Southern extension of locality and geological map, text-fig. 2a.

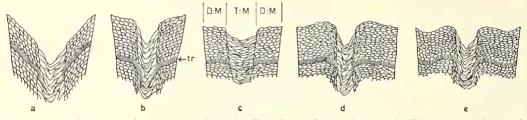
(a) Lateral denticles. These may be formed by individual fibres continuing a little beyond the face of the septum, or by the temporary lateral divergence of part of a trabecula from its upward direction of growth.

(b) Septal flanges. These are parallel to the growing edge of septum, and are formed by the lateral divergence in unison of all the trabeculae in a septum. In *Acanthophyllum*, for example, they slope downwards towards the axis. Their greatest development is frequently within the tabularium.

(c) Axial processes. These are usually difficult to interpret because of their complexity, but appear to be formed either by the irregular extension of trabeculae beyond the axial edge of the septum, or by irregularities in the course of the flanges in the axial region. The latter would appear to be the most common.

(d) Naotic plates. These are much as in *Craterophyllum*; they occur in *Pseudochono-phyllum*, some *Dohmophyllum*, and occasionally in other genera.

(e) Finally, in some instances the septa peripherally break up into parallel strands, each consisting of a single series of trabeculae. These strands are usually anastomosing, and in some cases may be modified and extended flanges.



TEXT-FIG. 3. Diagrammatic representation of calical forms in the Spongophyllidae, shown in longitudinal section, with German terms as used by Birenheide (1961, 1962) and the equivalent terms used herein. *a*, 'Trichterkelch': inversely conical calice (characteristic of *Acanthophyllum* (*Neostringophyllum*), *A*. (*Grypophyllum*)); *b*, 'Krempenkelch': bell-shaped calice (characteristic of *A. (Acanthophyllum*)); *c*, 'Flachkelch': saucer-shaped calice; *d*, 'Wulstkelch': everted calice; *e*, 'sattelrandiger Wulstkelch': everted calice with flared rim. D:M—dissepimentarium; T:M—tabularium. Note the correlation between arrangement of horizontal elements, attitude of trabeculae, and shape of calice.

Tabulae. The tabulae may be flat to gently concave, and mostly complete, as in *Spongophyllum*, or gently to deeply concave with a median depression, in some cases strongly infundibuliform, as in *Acanthophyllum* and *Xystriphyllum*. In the second case, the tabulae are generally predominantly incomplete to vesicular.

Dissepiments. Characteristically the dissepimentarium is wide, and consists of numerous small, globose to elongate dissepiments. Lonsdaleoid dissepiments are common. In *Spongophyllum* the dissepimentarium is comparatively narrow, but the presence of well-developed lonsdaleoid dissepiments is characteristic, and serves to link the genus with the group around *Acanthophyllum* with wide dissepimentaria.

Genus ACANTHOPHYLLUM Dybowski 1873

- 1873 Acanthophyllum Dybowski, p. 339 (fide Lang, Smith, and Thomas 1940, p. 13).
- 1961 Acanthophyllum Dybowski 1873; Birenheide, p. 80; contains an extensive synonymy to 1958.
- 1949 Pseudochonophyllum Soshkina, p. 119 (non Soshkina 1937).
- 1962 Acanthophyllum Dybowski 1873; Philip, p. 184 (partim).
- 1964 Grypophyllum Wedekind 1922; Pedder, p. 439 (partim).

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Type species. Cyathophyllum heterophyllum Edwards and Haime 1851, p. 367, pl. X, fig. 1; subsequent designation Schlüter, 1889, p. 296 (for description see Birenheide 1961, pp. 81, 89).

Diagnosis. Solitary, predominantly subcylindrical corals with more or less frequent growth swellings. Calice inversely conical or bell-shaped. Septa trabecular, thin or dilated, generally of only one radial series of trabeculae; lamellar thickening may occur in some or all growth stages; flanges, lateral denticulae, and axial processes common. Septa radial, or directed to a generally short median plane, frequently marked by elongation of the cardinal septum. Tabulae incomplete to vesicular, forming concave floors with a median depression. Lonsdaleoid disseptiments may be well developed.

Remarks. I follow Birenheide (1961) in subdividing the genus into three subgenera, distinguished on calical shape, degree of septal dilatation, and to a lesser extent degree of development of lonsdaleoid dissepiments. All three appear to be present in the Garra Formation. *Acanthophyllum mansfieldense* of Philip (1962) is a species of *A. (Neostringo-phyllum)*, and is therefore the earliest representative of that subgenus yet known. Similarly, the earliest *A. (Acanthophyllum)* would seem to be that described by Philip (1962) from the Gedinnian or Siegenian of Victoria. The Garra record of *A. (Grypo-phyllum)* would seem to be the earliest yet known for that subgenus.

The Russian records of this group are a little difficult to interpret. Most of the specimens placed by Soshkina (1949, p. 119; 1952, p. 98) in *Pseudochonophyllum* are *Acanthophyllum*. Bulvanker (1958) described several species under the names *Acanthophyllum*, *Neostringophyllum*, *Grypophyllum*, and *Stenophyllum*, but also included species better placed in other genera of this family. Similarly, species of *Acanthophyllum* are placed by Soshkina and Dobrolyubova (in Orlov 1962) in *Ptenophyllum*, *Acanthophyllum*, *Stenophyllum*, *Neostringophyllum*, and *Grypophyllum*.

Subgenus ACANTHOPHYLLUM Dybowski 1873

Type species. See above.

Diagnosis. Subgenus of *Acanthophyllum* with bell-shaped calice. With thin peripheral stereozone, few lonsdaleoid dissepiments. Septa generally weakly to strongly fusiform, frequently further thickened during ontogeny by lamellar sclerenchyme. Trabeculae arranged in half-fans in dissepimentarium.

Remarks. According to Birenheide (1961, p. 128), A. (Acanthophyllum) characterizes the Eifelian of the Eifel. In Australia species are known as early as the Gedinnian or Siegenian, and if recent interpretations are correct (Philip 1960; Philip and Pedder 1964), are not certainly known above the lower Eifelian. Of the five species so far assigned to Acanthophyllum s.l., four are herein considered to be A. (Acanthophyllum). These fall into two groups, one of large corallites and the other of small ones. The small species are A. (A.) aequiseptatum Hill 1940, and A. (A.) asper Hill 1940, both from the Murrumbidgee limestones (see pl. 85, figs. 1, 2). Both have Dc = circa 2 cm., n = circa 60. The holotypes differ in the manner of dilatation of their septa (strong, axially thickened, and convoluted, major more than minor, in A. (A.) asper; moderate, fusiform, uniform, in A. (A.) aequiseptatum), and in Dt (circa $\frac{1}{2}Dc$ in A. (A.) asper, circa $\frac{1}{4}Dc$ in A. (A.) aequiseptatum). However, I have collected several corallites from Clear Hill, type locality of A. (A.) aequiseptatum, which suggest that these

characters are rather variable, and that in fact the two species may be synonymous. This will require further study outside the scope of this paper.

The large Australian species are A. (A.) clermontense (Etheridge fil. 1911) from Clermont, Queensland, and A (A.) mansfieldense (Dun 1898) from Mansfield, Victoria. The former is solitary to weakly fasciculate, the latter trochoid. Both have Dc over 2.5 cm., the former reaching 6 cm. In both, Dt = circa $\frac{1}{4}$ Dc. In A. (A.) clermontense, n = 80 (max.), in A. (A.) mansfieldense n = 50. Their most important distinction is in their septal dilatation: in the former the septa are fusiform, and axially dilated and contorted; in the latter the dilatation is in the form of concentric series of wedges increasing in size peripherally, while the septa are radial, and not greatly dilated or contorted axially.

The new species described below belongs with this second group. It is easily distinguished from the previous species by the greater width of its oval tabularium, by the strongly bilateral arrangement of its septa, and by its deeply infundibuliform tabulae.

Acanthophyllum (Acanthophyllum) aeneae sp. nov.

Plate 85, figs. 5a, b

Derivation of name. Aeneas, a Graeco-Roman mythological hero.

Holotype. SU 11291 (Pl. 85, figs. 5a, b); loc. Be-10.

Diagnosis. Large A. (*Acanthophyllum*) with wide, oval tabularium of deeply infundibuliform incomplete tabulae; septa unequal, directed towards long axis of tabularium, moderately dilated; minor septa long, very unequal.

Description. Solitary, trochoid, or ceratoid. The external characteristics are unknown, as all free corallites collected were worn. The epitheca is apparently thin and lined with a narrow fibrous stereozone. As deduced from longitudinal sections, the calice is the bell-shaped one characteristic of the subgenus (see text-fig. 3), with a fairly wide sloping rim and a wide, funnel-shaped axial pit. The greatest known diameter is 3.6 cm. + (estimated *circa* 4.5 cm.), but most corallites are about 2 cm. across.

Dimensions. In mm. of representative specimens.

No.	loc.	Dc	Dt	Dt/Dc	п
SU 11291*	Be-10	est. 45	15×22	ca. 0.3-0.5	ca. 74
SU 11296	,,	18.5 +	7×7.5	?	ca. 60
SU 14121	Ct-6	est. 38	6.5	ca. 0.2	ca. 60

*Holotype; measured Dc = 36 mm.

Adult corallites have some 60–70 septa. The major septa are long and unequal, extending to the axis where they are arranged about a long median plane. This plane is further delineated by an elongate septum (cardinal?) at one end, which is flanked by long minor septa. Opposite may be a rather short major septum. The septa are fusiform and moderately to strongly dilated; the dilated septa at most are equal to the interseptal loculi. The septa are rough-sided, but not markedly flanged in the dissepimentarium; thick flanges are prominent in the tabularium, where they are gently axially inclined. In the zone of maximum septal dilatation there may be intermittent reinforcement by lamellar sclerenchyme, which spreads over the surfaces of adjacent dissepiments (here strongly geniculate towards the periphery), so that an incomplete zigzag stereozone

may form. In large corallites there may be two or three concentric stereozones so formed. The dilatation is somewhat variable within even the same transverse section; however, the major and minor septa are generally equally dilated. The minor septa vary in length, generally ending at the inner margin of the dissepimentarium, but at times somewhat withdrawn or extending a little way into the tabularium.

The septal structure is of fine trabeculae, approximately parallel, and diverging from the median plane of the septum. They are arranged in a broad half-fan within the dissepimentarium, the maximum inclination at the margin of the tabularium being about 50° from the vertical. The arrangement within the tabularium is less clear, but seems to consist of a much less divergent half-fan, the trabeculae being nearly vertical near the dissepimentarium, becoming moderately axially inclined (about 20° from the vertical?) near the axis. The flanges are trabecular and are perpendicular to the direction of growth of the trabeculae. Even in longitudinal section they can be readily distinguished from the lamellar sclerenchyme reinforcing the septal dilatation.

The epitheca has been worn from all available specimens, so the relative width of the tabularium is uncertain. It does appear to be rather wide (see table of dimensions). In all specimens the tabularium is markedly oval, the long axis being in the presumed counter-cardinal plane. The tabular floors are funnel-shaped, with sides inclined axially at about $30-40^{\circ}$ from the horizontal; the margins are upturned, at times sharply, while there is a strong axial depression about $\frac{1}{4}$ Dt across, and as deep. The tabulae are close, elongate, varying from nearly complete to incomplete (particularly marginally and within the axial depression).

The dissepimentarium consists of numerous small rather globose to elongate vesicles, which increase in inclination but decrease in size towards the axis. There is a definite region towards the tabularium where the rate of increase in inclination is temporarily increased. This change in slope is, however, not quite as abrupt as in the German species of *Acanthophyllum* s.s. In transverse section the dissepiments are strongly geniculate, the apices directed peripherally, over the greater part of the dissepimentarium. Lons-daleoid dissepiments do not appear to be developed, but it is possible that complete specimens may show a narrow peripheral series.

Comparison. A. (A.) aeneae differs from the two other large Australian species—A. (A.) mansfieldense (Dun 1898) and A. (A.) clermontense (Etheridge fil. 1911)—in its wide tabularium and in the extreme bilaterality of the septa and tabularium. A. (A.) clermontense has similar septal dilatation, except that the major are thicker, but the tabular floors are not as deeply infundibuliform; the species may be weakly colonial. A. (A.) mansfieldense has fewer septa which are dilated in a distinctive manner—concentric series of wedges—and somewhat withdrawn from the axis; the calix is considerably shallower.

The closest German species is the type A. (A.) heterophyllum (Edwards and Haime 1851); this has rather more septa which are generally markedly convolute axially, and not nearly so strongly bilaterally arranged; moreover, the minor septa are thinner than the major. The tabulae are smaller, rather more globose, and not so steeply inclined. Similarly, the dissepiments are more globose, and are more elongate axially, whereas in A. (A.) aeneae they are more elongate peripherally. The manner of reinforcement of the septal dilatation by sclerenchyme differs somewhat from the German species.

Known localities. Be-10, Ct-6, Ct-53.

Acanthophyllum (Acanthophyllum) clermontense (Etheridge fil. 1911)

- 1911 *Cyathophyllum*(?) *clermontensis* Etheridge, p. 5, pl. B, figs. 1, 2, pl. D, fig. 3. Douglas Ck., Clermont, Queensland; 'Upper Couvinian'.
- 1939b Acanthophyllum clermontense Etheridge; Hill, p. 57, pl. IV, figs. 1, 2.

non 1962 Acanthophyllum clermontense (Etheridge); Philip, p. 185, pl. 27, figs. 1, 2. Tyers R., Victoria; Gedinnian.

Diagnosis. Large, solitary or weakly fasciculate *A*. (*Acanthophyllum*) with narrow tabularium; septa moderately dilated, fusiform, frequently with second zone of fusiform dilatation just outside tabularium, generally axially contorted; tabulae incomplete, forming bowl-shaped floors with wide axial deepening.

Remarks. This of all the Australian species most resembles the German species as described by Birenheide (1961); from them it differs particularly in being weakly fasciculate, but also in its narrow tabularium (Dt/Dc = $circa \frac{1}{4}$). The specimen described and figured by Philip (1962) from Victoria has distinctly domed tabular floors and apparently an inversely conical calice; it is probably a species of *Dolumophyllum* Wedekind 1923 (see Birenheide 1963), although somewhat older than described species of the genus.

A. (A.) sp. cf. clermontense (Etheridge fil. 1911)

Plate 85, figs. 3, 4, 6, Plate 86, fig. 1; text-fig. 4.

Material. Several specimens (9 sectioned) from locs. Cr-100, P-43.

Description. Most of the specimens appear to be solitary, ceratoid to cylindrical, but one at least (SU 13230, loc. Cr-100) is clearly fasciculate, consisting of a small radiating corallum of 3 or 4 corallites, increase being peripheral. The epitheca is thin, marked by narrow septal grooves. Repeated sharp rejuvenescence rims often occur. The calice has a wide, sharp-rimmed, gently sloping border, and a rather shallow, bowl-shaped axial pit. The septa form prominent ridges on the floor of the calice. The largest known corallite is about 3 cm. in diameter, but for most corallites Dc = 15-20 mm.

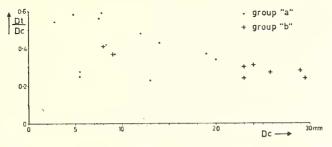
In adults n = 50-58. The major septa are long, extending unequally to the axis. Their axial structure and arrangement is variable: in some they are thin, with thin flanges, and are irregularly curved as in A. (A.) clermontense; in others, the arrangement is similar, but the septa are rather thickened, and heavily flanged. This leads on to those specimens in which the septa are thick and strongly flanged axially, and are bilaterally directed to a short median plane, rather than rotated as in typical A. (A.) clermontense.

Dimensions. In mm. of representative specimens.

No.	loc.	Dc	Dt	Dt/Dc	п
Group a: septa no	ot greatly d	ilated or flat	nged:		
SU 13227	Cr-100	est. 22	5.5	<i>ca</i> . 0·25	54
SU 13230*	,,	4 ·8	2.8	0.58	38
"	,,	est. 20	6.7	<i>ca</i> . 0·34	58
Group b: septa st	rongly dilat	ed and flang	ged:		
SU 17237	P-43	est. 24	7.5	ca. 0·31	54
SU 17258	"	est. 23	7·0	<i>ca</i> . 0·30	52
SU 17261	,,	est. 29.5	7.0	<i>ca</i> . 0·24	52?
* colonial.					

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Similarly, the septal dilatation is highly variable, even in the one transverse section. Generally the minor septa are as thick as the major and terminate at the margin of the tabularium. In some specimens the septa are fusiform in transverse section, and only moderately dilated, with broad wedge-shaped bases. Other specimens show this type, and as well strongly dilated septa tapering inwards from the thick bases, with perhaps a second zone of thickening corresponding to the zone of fusiform dilatation of the thinner septa. The other extreme (group b in the above table) is of extremely dilated septa, in contact over the outer half to two-thirds of the dissepimentarium, and then tapering inwards, perhaps with a narrow zone of slight fusiform dilatation just outside the tabularium. Occasionally in these specimens some of the septa are peripherally attenuate, but rapidly dilate inwards, being in contact a short distance in from the epitheca. The septa in some sections bear fine lateral denticulae, and in most cases are



TEXT-FIG. 4. A. (Acanthophyllum) sp. cf. clermontense. Scatter diagram for Dt/Dc:Dc.

flanged; the inclination of the flanges increases inwards to the margin of the tabularium and then decreases to nearly horizontal. The flanges are generally weak but may become strong in the tabularium.

The septa consist of thin trabeculae arranged in broad half-fans in the disseptimentarium: near the periphery they are directed upwards and inwards at a small angle from the vertical. This angle increases steadily inwards until near the tabularium, where there is a sudden fairly marked increase to about $30-40^\circ$; within the tabularium they are directed more nearly vertically as the axis is approached.

In juveniles the tabularium is wide, Dt = circa 0.5Dc; however, it increases in width more slowly than the corallite, so that in adults it is narrow (*circa* 0.3–0.4Dc)—see text-fig. 4. The tabulae are generally incomplete, axially inclined, and only moderately convex. The tabular floors are bowl-shaped, with upturned margins, and a wide, shallow axial depression.

The dissepimentarium in adults is wide, consisting of numerous series of small dissepiments. In the outer zone these are gently to moderately axially inclined and rather globose. In a narrow zone around the tabularium they are steeply axially inclined and tend to be elongate. Lonsdaleoid dissepiments are almost entirely absent; in only one or two sections have I seen a few small ones.

Remarks. These specimens differ from the Clermont ones in their smaller size, and in their far more variable septal structure, dilatation, and axial arrangement. Were it not for the gradation shown by some specimens I would be inclined to place those with axially dilated and flanged septa directed to a short axial plane (group b in the table of

dimensions) into a distinct species. Until the extent of variation in the Clermont species is known fully, and until considerably more Garra material is available, it is possible only to compare them.

Known localities. Cr-100 (9 or 10 specimens), P-43 (5 or 6 specimens), WC-9. Possibly also Cr-77.

Subgenus NEOSTRINGOPHYLLUM Wedekind 1922

Type species. By monotypy, *N. ultimum* Wedekind 1922, p. 16, figs. 17, 18. Type locality: Düsseltal, Bergisches Land; upper Givetian.

Diagnosis. Subgenus of *Acanthophyllum* with inversely conical calice. Epitheca thick; septa predominantly strongly dilated, composed of trabeculae directed upwards and inwards, approximately parallel. Lonsdaleoid dissepiments absent or poorly developed. Tabulae mostly incomplete, vesicular.

Remarks. None of the named Australian species can be certainly placed herein. However, several specimens, from a number of basins, previously referred to *Acanthophyllum aequiseptatum* Hill 1940, are actually representatives of *A*. (*N*.) *implicatum* sp. nov. If this subgeneric assignment is accurate—and there are no marked morphological differences from the German species as figured by Wedekind (1922), Walther (1928), and Birenheide (1961)—then this is a very early appearance of the subgenus, for in Germany and in England (Webby 1964, p. 12) it is characteristic of the Givetian. The Australian occurrences are all Lower or basal Middle Devonian. Homomorphy is possible, but for the present I consider it best to use the one subgeneric name, as in both cases the species are probably derived from *A*. (*Acanthophyllum*), and so are closely related.

Acanthophyllum (Neostringophyllum) implicatum sp. nov.

Plate 86, figs. 2-8; text-figs. 5, 6

- 1940b Acanthophyllum sp. Hill, p. 253, pl. 9, fig. 6. Wee Jasper, N.S.W.; Emsian or Eifelian.
- 1940c Acanthophyllum spp. Hill, p. 152, pl. 2, fig. 2; ?p. 153, pl. 2, figs. 3a-c. Silverwood, S. Qld.; 'lower Couvinian' (Emsian?).
- 1940 Acanthophyllum sp. Hill and Jones, p. 179, pl. 2, figs. 1, 2. Molong District, N.S.W.; Emsian?
- 1942b Acanthophyllum sp. Hill, p. 14, pl. 1, figs. 2a, b. Mt. Etna, Qld.; Emsian?
- ?1942b Acanthophyllum sp. or Lyrielasma sp. Hill, p. 14, unfigured. Mt. Etna, Qld.
- ?1942d Acanthophyllum cf. mansfieldense (Dun); Hill, pp. 182, 183, pl. 5, fig. 1. Wellington, N.S.W.; Emsian?
- 1942*d* Acanthophyllum aequiseptatum Hill; Hill, p. 183, pl. 6, figs. 1*a*, *b* (non Hill 1940b, p. 251). Wellington, N.S.W.
- 1950 Acanthophyllum sp. Hill, p. 139, pl. 5, fig. 2. Buchan, Vic.; Emsian? (or early Eifelian?).
- 1962 Acanthophyllum aequiseptatum Hill; Philip, p. 184, pl. 26, figs. 2, 3. Tyers R., Vic.; Gedinnian (or Siegenian?).

Derivation of name. Latin *implicatus* = entangled, confused; referring to the septal meshwork at the base of the calice.

Holotype. SU 17219 (Pl. 86, figs. 2a, b). Type locality: P-40.

Diagnosis. Small A. (*Neostringophyllum*) with deep, inversely conical calice whose base is filled with an extensive meshwork of septal ends and flanges; septa moderately to extremely dilated, flaring to wedge-shaped peripherally, tapering inwards, without

secondary lamellar deposits; tabularium rather wide, consisting of moderately to deeply concave incomplete tabulae, generally with a small axial deepening.

Description. Solitary; corallites may form loose colonies of adherent individuals, frequently invested by a stromatoporoid. Corallites attach themselves by lateral expansions of the dissepimentarium (Pl. 86, figs. 2, 8). They are ceratoid to cylindrical, with irregular although not pronounced growth swellings and contractions; occasional rejuvenescence rims occur. The calice is deeply inversely conical, with a sharp rim, steep sides, and a concave base. The septa extend as low ridges down the sides, but at the base form a deep meshwork of lamellae and flanges, whose upper surface is gently concave, and up to 10 mm. above the topmost tabula (Pl. 86, figs. 4, 7). For normal adults, Dc = 10-20 mm.; the maximum known is 22.5 mm.

Dimensions. In mm.

No.	loc.	Dc	Dt	Dt/Dc	п
SU 17219	P-43	2.5	1.4	0.56	30
,,	,,	9.6	ca.0.5	<i>ca</i> . 0.52	48
,,	,,	12.4	6.0	0.48	56
••				ca. 0.44	56
,,	,,	14.0	<i>ca</i> . 0.6	<i>ca.</i> 0.43	50

Measured from random sections of corallites in type specimen.

There are up to 66 septa, the usual number lying between 48 and 62. Generally they are equally dilated and straight in the dissepimentarium, to which the minor septa are confined; within the tabularium the major septa may be straight, but are more usually curved. They are frequently arranged in four ill-defined groups, apparently symmetrical about the counter-cardinal plane. This plane is frequently marked by elongation of the cardinal septum, which is often then flanked by elongate minor septa. Septal dilatation is quite variable in extent, at times even within the one corallite. It is generally moderate to strong, tapering inwards; the septal bases are generally flared or wedge-shaped, forming a stereozone which is usually about 0.5-1 mm. across, but may rarely be up to 3 mm. wide. In a few cases the septal bases do not contact at all, when there is between them a fibrous stereozone about 0.3 mm, thick. In some sections the septal dilatation is slightly fusiform or lanceolate. As the septal dilatation decreases inwards, so there is a steady increase in the degree of lateral flanging; these flanges are trabecular outgrowths, parallel to the calical surface, and perpendicular to the direction of the trabeculae. They are steeply axially inclined in the disseptimentarium, the inclination decreasing in the tabularium, such that they are best seen in slightly oblique longitudinal sections. The combination of rotated or convoluted septal ends and flanges frequently presents a highly complex picture in transverse sections of the tabularium.

The septa are composed of thin trabeculae directed upwards and inwards at about 30° to the horizontal in the dissepimentarium. This inclination changes rapidly as the septa enter the tabularium, so that they are nearly vertical. Variation in the length of the component fibres produces fine lateral denticulae on the septal sides in many specimens.

The tabularium in adults is about 0.4-0.5 Dc. It consists of slightly convex incomplete tabulae, generally increasing a little in size axially; these are arranged in gently to deeply

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concave tabular floors, with upturned margins, and generally with a narrow median depression of variable depth.

The dissepimentarium consists of up to 9 series of small, globose to rather elongate, highly inclined dissepiments. The inclination may be uniform, or may increase gradually towards the axis; there is, however, never the marked change in inclination from moderate to almost vertical near the tabularium which characterizes species of *A*. (*Acanthophyllum*). Only in relatively few cases is the increase in inclination sufficient for the dissepiments at the inner margin of the dissepimentarium to be vertical. Lonsdaleoid dissepiments are not developed.

Variation. This species shows considerable variation, particularly in the degree and manner of septal dilatation—features which unfortunately do not lend themselves to statistical analysis. In some specimens the septa are uniformly thin, and change little in thickness inwards, beyond the characteristic peripheral wedge-like or flaring dilatation. At the other extreme are those corallites in which the septa are in contact peripherally for up to 3 mm., then taper inwards, but remain thick even in the tabularium. As well, dilatation varies from the usual inwards taper to moderately lanceolate (maximum dilatation at mid-length), again always with a peripheral expansion.

Further variation occurs in the degree of inclination of the disseptiments. This varies from about 30° to about 45° from the vertical. The concavity of the tabular floors also varies within wide limits.

Measurements of Dc, Dt, and n were made for 77 individuals. As this was done from thin sections, the majority of which were consciously made of adult corallites, simple frequency plots are of slight value. Graphs were plotted for Dt:Dc (text-fig. 5a) and for n:Dc (text-fig. 6). The former is the most significant: there is relatively little scatter, and straight-line axes show a definite change in slope at Dc = 10 mm. This is taken to represent the boundary between juvenile and adult corallites. For the juveniles, Dt =0.5Dc; for adults, Dt = 0.33Dc+1.67 approximately. There is greater scatter in the plot of n:Dc, but here also there seems to be a distinct break in slope at Dc = circa 10 mm.

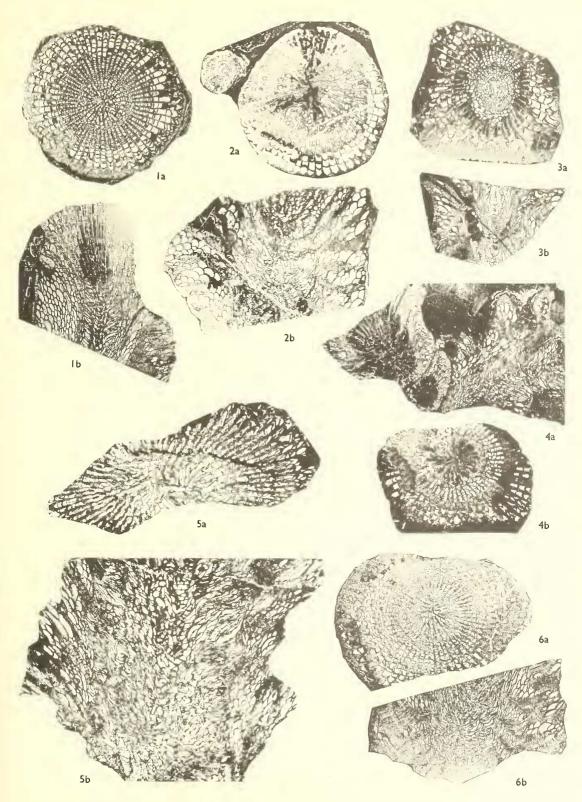
A plot of Dt/Dc:Dc shows a fair degree of scatter (text-fig. 5b). Dt/Dc changes gradually from about 0.5–0.6 for juveniles to about 0.4–0.5 for most adults; very large corallites may have a tabularium as narrow as 0.33 Dc.

All figures $\times 2$.

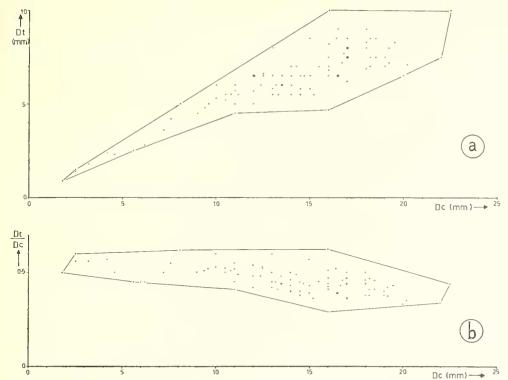
EXPLANATION OF PLATE 85

- Fig. 1. A. (Acanthophyllum) aequiseptatum Hill 1940. 1a, b, transverse and longitudinal sections, holotype AM F 9577, Bluff Limestone, Clear Hill, Taemas, N.S.W. Photographs by courtesy of the Australian Museum, Sydney.
- Fig. 2. A. (A.) asper Hill 1940. 2a, b transverse and longitudinal sections, holotype UQ F 4270, Wee Jasper, near Taemas, N.S.W. Photographs supplied by Mr. J. Jell, University of Queensland.
- Figs. 3, 4. *A*. (*A*.) sp. cf. *clerniontense* (Etheridge fil. 1911), group *a* (see pp. 552–3). 3*a*, *b*, transverse and longitudinal sections, SU 13227, loc. Cr–100. 4*a*, longitudinal section of a small colony, 4*b*, transverse section of the corallite on the right in 4*a*; SU 13230, loc. Cr–100.
- Fig. 5. A. (A.) aeneae sp. nov. 5a, b, transverse and longitudinal sections, holotype SU 11291, loc. Be-10.

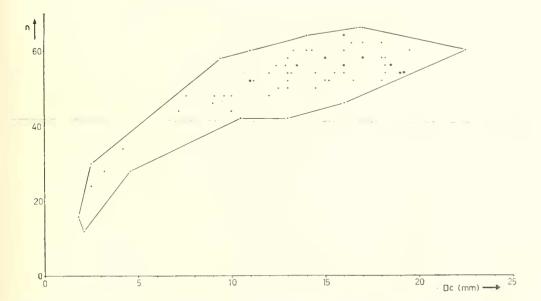
Fig. 6. A. (A.) sp. cf. *clermontense*, group b (see pp. 552–3). 6a, b, transverse and longitudinal sections, SU 17237, loc. P–43.



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TEXT-FIG. 5. *A.* (*Neostringophyllum*) *implicatum* sp. nov. Scatter diagrams and limiting polygons showing variation of (*a*) Dt:Dc, and (*b*) Dt/Dc:Dc.



TEXT-FIG. 6. A. (Neostringophyllum) implicatum sp. nov. Scatter diagram and limiting polygon for n:Dc.

Remarks. The strongest objection to placing this species in *A. (Neostringophyllum)* is that in the Eifelian succession the earliest known species, *A. (N.) concavum* (Walther 1928), appears at the Eifelian–Givetian boundary (see Birenheide 1961, p. 128). However, there appears to be no significant morphological difference between the German and Australian species; I feel it is unwise at this juncture to erect an endemic Australian genus solely on the basis of apparent age.

Range. This species is now known from a number of localities in eastern Australia. It is likely that most of these are Coblenzian in age. Hill (1940b) suggested an age about the boundary of the Lower and Middle Devonian for the Bluff Limestone fauna of the Taemas region. Philip and Pedder (1964) have forcefully suggested a Siegenian or perhaps early Emsian age for this succession. Similarly, they consider the Buchan sequence to be mainly Siegenian, as against Hill's (1950) late Emsian or early Couvinian. The two limestones have very similar faunas, including A. (A.) aequiseptatum and A. (N.) implicatum.

The Silverwood fauna, Hill (1940c) compared most closely within Australia with that of the Nemingha Limestone of Tamworth: the latter she (1942c) considered to be probably late Lower Devonian, while the former she placed in the lower Couvinian. I consider them both to be Coblenzian; A. (N) *implicatum* occurs at Silverwood, but is not yet known from Tamworth. It is also known from the Mt. Etna Limestone of Queensland, which is quite close to the Garra faunally, and which Hill (1942b) considered to be (at least in part) Coblenzian in age.

The oldest fauna containing A. (N.) *implicatum* is apparently the Tyers R. fauna of Victoria, which Philip (1960, 1962) considers to be Gedinnian or possibly early Siegenian.

A. (N.) implicatum would therefore seem to be characteristic of the Lower Devonian faunas of eastern Australia.

Known Garra localities. A. (*N.*) *implicatum* is widespread in the Garra Formation, second perhaps only to the digonophyllids. It has been collected from the following localities: Br–3, Br–10, Ca–1, Cr–1, Cr–2, Cr–5, Cr–86, Cr–89, Cr–94, Cr–100 (very common), Cr–103, Cr–106?, Cr–111, Ct–16?, Ct–55?, E–5, E–37?, Ge–3 (very common), Ge–7b (common), Ge–12?, Gn–7?, MM–1, MM–5b, MM–6, MM–7, MM–11, P–22 (rather common), P–23, P–25, P–26, P–38 (rather common), P–40 (type locality), P–43 (abundant), WC–4, WC–5; BR¹/177, BR¹/965?

EXPLANATION OF PLATE 86

Fig. 1. A. (Acanthophyllum) sp. cf. clermontense (Etheridge 1911), group b (see pp. 552–3). Longitudinal section through calice, SU 17258, loc. P–43; ×2.

Figs. 2-8. A. (Neostringophyllum) implicatum sp. nov.

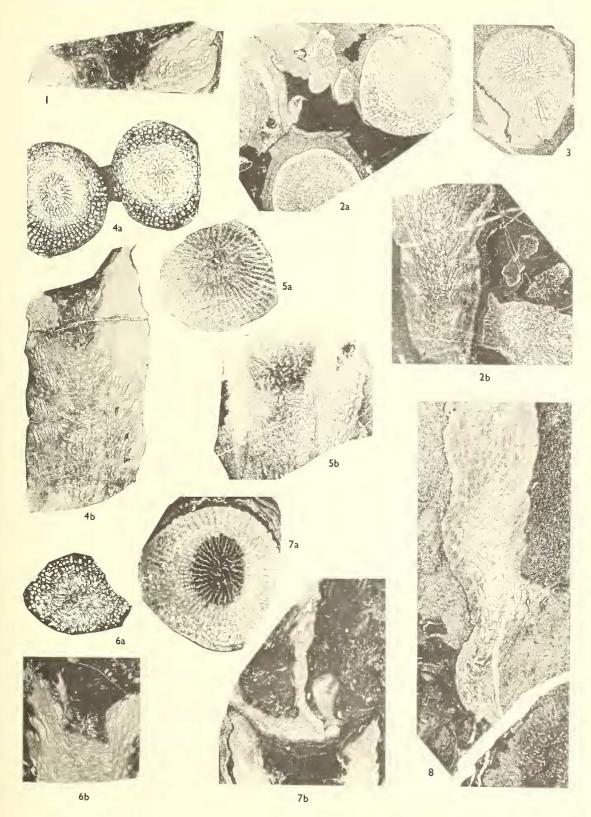
2*a*, *b*, transverse to longitudinal sections of a group of corallites invested by a stromatoporoid; holotype SU 17219, loc. P-40; $\times 2$. 3, oblique transverse section, SU 15296, loc. E-5; $\times 2$. 4*a*, transverse section, 4*b*, longitudinal section showing septal mesh in calice; SU 7297, loc. Ge-3; $\times 2$. Figured Hill 1942*d*. 5*a*, *b*, transverse and longitudinal sections, SU 18222, loc. P-43; $\times 2$.

6a, b, transverse and longitudinal sections of a specimen with septa thickened in the tabularium, and with nearly flat tabular floors; SU 12177, loc. Ca-1; $\times 2$.

7*a*, transverse section low in calice, showing septal mesh, 7*b*, longitudinal section; UCT F 1983, loc. P-43; $\times 2$.

8, longitudinal section of a juvenile corallite adherent to the surface of a stromatoporoid colony; SU 13222, loc. Cr-100; \times 4.

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Acanthophyllum (Neostringophyllum) turni sp. nov.

Plate 87, figs. 1, 2; text-fig. 7

Derivation of name. Turnus, commander of the Latins resisting Aeneas' settlement in Italy. *Holotype*. SU 14247 (pl. 87, figs. 1*a*, *b*). Type locality: Ct–44.

Diagnosis. Small *A.* (*Neostringophyllum*) of irregular growth shape, with frequent sharp rejuvenescence rims; septa dilated to contact at periphery, and intermittently as inverse cones of septal tissue and sclerenchyme; the degree of dilatation increases distally. Tabularium fairly narrow, of concave incomplete tabulae, often axially deepened. Dissepiments steeply inclined, elongate.

Description. The solitary corallite is generally curved, ceratoid to trochoid, with marked growth irregularities; it is commonly oval to irregular in cross-section. Rejuvenescence is generally frequent and strong, forming sharp rims which are often close, so that the contracted intervening spaces are deep but almost slit-like (see text-fig. 7). The calice is deep, inversely conical, with a sharp rim and a narrow concave apex; the septa form only low ridges on its sides and floor. The epitheca, apart from transverse growth irregularities, is marked by narrow septal grooves.

Adult corallites are about 15-20 mm. in diameter.

Dimensions. In mm. of representative corallites.

No.	Dc	Dt	Dt/Dc	н
SU 14247*	8.6	4.8	0.56	38
,,	est. 15	7.0	0.47	50
SU 14248	16.4	5.9	0.36	66
SU 14250	15.5	6.5	0.42	52

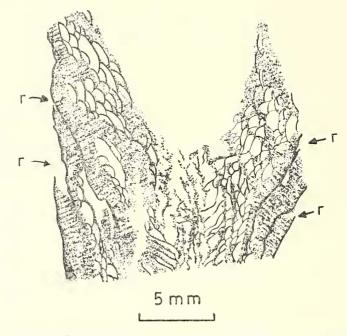
*Holotype; all specimens from loc. Ct-44. Mean values of Dc are given for oval corallites.

In adult corallites there are usually 50–64 septa. These extend inwards from the epitheca (0.03 mm, thick), unbroken by lonsdaleoid disseptments; the major septa generally almost reach the axis, where they are usually directed to a prominent countercardinal plane. There may be slight to moderate rotation of the septal ends. The counter and cardinal septa are elongate, but do not meet. The shortest major septa flank these, and the septal length gradually increases away from these, being again greatest transverse to the counter-cardinal plane. The minor septa tend to be irregular in length, although on the whole they extend inwards for about R/2. Those flanking the counter (or cardinal?) septum may be somewhat lengthened. The septa are dilated to contact in a peripheral stereozone about 1-1.5 mm, wide, whose inner surface is reinforced by lamellar sclerenchyme. In this narrow region of reinforcement the septa themselves attenuate rapidly inwards, so that inside the stereozone they are thin or only weakly dilated, in the latter case being irregular to fusiform. In most corallites inversely conical sheets of sclerenchyme extend inwards from the stereozone, coating septa and dissepiments. These appear to correspond in position to prominent and very close rejuvenescence rims, seemingly representing tissue deposited on the surface of the calice immediately before constriction, and to the peripheral stereozone lining the epitheca of the immediately subsequent expansion (see text-fig. 7).

The septa are generally somewhat wavy and bear moderately developed flanges,

which increase in frequency in the tabularium. Axial processes are weakly developed or absent, as are lateral denticulae.

The septal microstructure is that typical for the subgenus: approximately parallel fine monacanthine trabeculae directed upwards and inwards at 20–30° from the horizontal within the dissepimentarium, the inclination becoming much steeper in the tabularium.

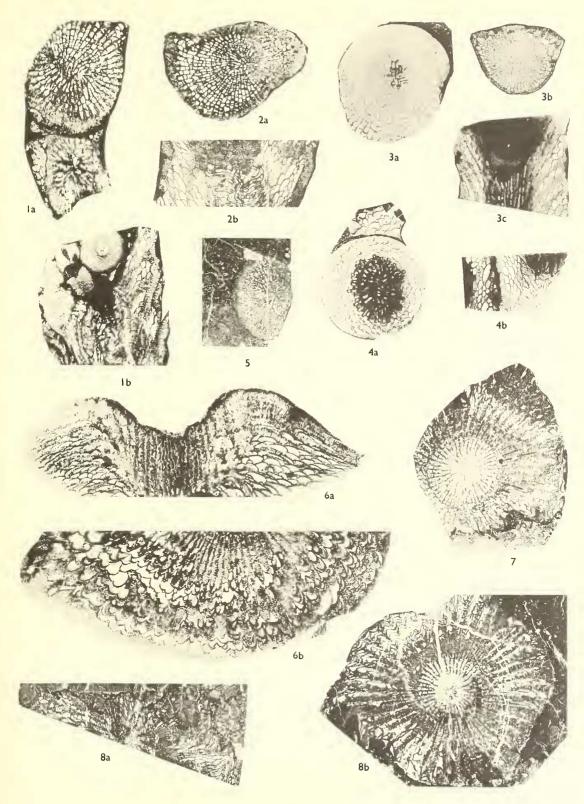


TEXT-FIG. 7. A. (*Neostringophyllum*) turni sp. nov. Longitudinal section of holotype SU 14247, ×4, showing sharp rejuvenescence (r) above deep, slit-like re-entrants, and the associated inverse cones of septal dilatation. Drawn from photograph.

EXPLANATION OF PLATE 87

- FIGS. 1, 2. A. (*Neostringophyllum*) *turni* sp. nov. 1*a*, transverse and oblique sections, 1*b*, longitudinal section showing rejuvenescence (cf. text-fig. 7); holotype SU 14247, loc. Ct–44. 2*a*, *b*, transverse and longitudinal sections, SU 14248, loc. Ct–44.
- Figs. 3, 4. *A.* (*Grypophyllum*) *jenkinsi* sp. nov. 3*a*, transverse section at base of calice, 3*b*, transverse celluloid peel near proximal end, 3*c*, longitudinal section showing unflanged septa; holotype SU 16247, loc. Ge–2. 4*a*, transverse section showing septal thickening in tabularium, 4*b*, longitudinal section; UCT F 1947, loc. Ge–2.
- Fig. 5. Lyrielasma sp. cf. subcaespitosum (Chapman 1925). Transverse section, SU 19238, loc. St/2565.
- FIGS. 6–8. Pseudochonophyllum pseudohelianthoides (Sherzer 1892). 6a, b, off-centre longitudinal, and transverse sections, holotype, Rominger Collection, Museum of Paleontology, University of Michigan; Koněprusy, Bohemia. Photographs supplied by Prof. E. C. Stumm. 7, transverse section showing well-developed naotic plates (lower right), SU 13241, loc. Cr–100. 8a, b, longitudinal and transverse sections, UQ F 3412, Silverwood, Qld.; Acanthophyllum sp. cf. mansfieldense of Hill 1940c, pl. II, figs. 1a, b. Photographs by courtesy of Prof. D. Hill.

All figures $\times 2$.



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The tabularium decreases from about $\frac{1}{2}$ Dc in juveniles to about 0.4Dc in adults. The tabular floors are moderately to strongly concave, with upturned margins and an axial deepening which is apparently a little eccentric. The tabulae are incomplete, elongate, and only slightly domed. They are thin, or lightly to moderately coated with sclerenchyme in the conical zones of dilatation.

The dissepimentarium consists of up to ten series of small, fairly globose to elongate, highly inclined dissepiments. These are generally uniform in size and inclination, but may become vertical at the margin of the tabularium; this is generally not vertically persistent in a single corallite.

Variation. Data are too few for rigorous treatment; plots (not figured) were made for Dt:Dc, Dt/Dc:Dc, and n:Dc. The first two appeared to be straight-line plots, the first suggesting Dt = 0.4Dc+0.4. The plot for n:Dc was apparently curved, the rate of insertion of septa decreasing steadily with age of the corallite.

Comparison. On the basis of available material, this species is inseparable in size, number of septa, and relative width of tabularium from A. (N.) implicatum sp. nov., and from A. (Grypophyllum) jenkinsi sp. nov. (described below). Examination of the data plots suggests that further material may show that Dt/Dc is slightly less than for A. (N.) implicatum, from which it is distinguished by its prominent rejuvenescence, its septal dilatation, and its lack of an intricate septal meshwork axially. A. (G.) jenkinsi lacks the wide stereozone and sharp rejuvenescence; moreover, it may have some lonsdaleoid dissepiments distally. Both of these species lack the periodic conical dilatation characteristic of A. (N.) turni. In this feature it differs also from all of the European species.

Remarks. This species is placed in *A*. (*Neostringophyllum*) because of its peripherally strongly thickened septa and its complete lack of lonsdaleoid dissepiments.

Known localities. Ct-44, Ct-45.

Subgenus GRYPOPHYLLUM Wedekind 1922

Type species. G. denckmanni Wedekind 1922, p. 13, figs. 13, 14. Type locality: Bergisch–Gladbach, Bergisches Land; Büchel Beds, Givetian.

Diagnosis. Subgenus of *Acanthophyllum* with inversely conical calice, usually with fairly rounded margin. Septa predominantly thin, composed of fine trabeculae directed upwards and inwards, roughly parallel. Lonsdaleoid dissepiments, particularly interrupting minor septa only, common; dissepiments inclined uniformly inwards. Tabulae incomplete, vesicular.

Remarks. Hill (1940b, p. 267) interpreted *Grypophyllum* as fasciculate, and has described several species from Australia on this basis. Of these, '*G*.' *aggregatum* Hill 1940 and '*G*.' *lophophylloides* Hill 1942*a* I tentatively place in *Lyrielasma* Hill 1939. The other species from north Queensland assigned by Hill (1942*a*) to *Grypophyllum* have tabulae which suggest that they may not even be spongophyllids.

Pedder (1964, p. 439) followed Hill in interpreting the genus as fasciculate, and described a Canadian species which seems to be allied to 'G.' aggregatum Hill 1940,

both of which differ from typical *Lyrielasma* in their rather thin peripheral stereozone. For the present, however, I would leave them in that genus.

Acanthophyllum (Grypophyllum) jenkinsi sp. nov.

Plate 87, figs. 3, 4

Derivation of name. For Dr. T. B. H. Jenkins, of the University of Sydney.

Holotype. SU 16247 (pl. 87, figs. 3 a-c). Type locality: Ge-2.

Diagnosis. A. (*Grypophyllum*) up to 25 mm. across, with thin epitheca; minor septa well developed; cardinal and counter septa elongate; septal processes absent; lonsdaleoid dissepiments occur only in adult stage.

Description. Solitary, cylindrical or ceratoid, with some growth irregularities. The epitheca has distinct interseptal ridges and faint growth lines. The calice is inversely conical, rather deep, with a concave base. Septa form low ridges down its sides, and somewhat higher ridges across its base. The greatest known Dc = 23 mm.; it is usually about 15–20 mm.

Dimensions. In mm.

No.	Loc.	Dc	Dt	Dt/Dc	n
SU 16247*	Ge-2	8.5	4.0	0.47	48
,,	,,	10.9			50
• •	> ?	16· 0	5.0	0.31	56
,,	,,	16.5	5.2	0.32	56
UCT F 1947	,,	13.9	8.0	0.28	52

*Holotype: serial sections over a length of 40 mm.

In adults, n = 50-60. The septa are long, fusiform, and only slightly dilated. Their peripheral ends, however, expand rapidly as broad, blunt wedges, to form a dentate stereozone. The septal bases are slightly concave externally (in transverse section), so giving rise to the interseptal ridges of the epitheca. The septa are smooth, or bear fine lateral denticulae; they are gently waved on a small scale, appearing straight at first glance. Weak, discontinuous flanges occur near and in the tabularium. There are no axial processes. In juveniles the septa are complete, but in adults some peripheral discontinuities generally develop. The minor septa end just inside the tabularium. The major septa extend unequally to a fairly short median plane, which is marked by elongate counter and cardinal septa. The counter (?) septum is flanked by elongate minor septa.

The septa consist of fine almost parallel trabeculae directed upwards and inwards at about 20° from the horizontal. Their arrangement within the tabularium is unknown.

The tabularium is rather narrow—about 0.3Dc in adults, somewhat greater in juveniles. The tabular floors are concave and often moderately deepened axially. The tabulae are incomplete, elongate, and weakly convex.

The dissepimentarium consists of up to 9 series of globose to rather elongate dissepiments, steeply axially inclined. They are fairly uniform in size and increase in inclination only slightly towards the tabularium. Lonsdaleoid dissepiments, only rarely interrupting the major as well as the minor septa, are poorly developed in adult stages.

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Comparison. A. (G.) jenkinsi sp. nov. does not closely resemble any previously described Australian species. A. (N.) implicatum sp. nov. is at first glance rather similar, and their data plots coincide, but it may be distinguished by the different septal dilatation (tapering axially, and rather greater), and the complete lack of lonsdaleoid dissepiments; also it has a generally thicker epitheca and stereozone, and a wider tabularium. Finally, the septal mesh at the base of its calice is highly distinctive of A. (N.) implicatum.

A. (G.) jenkinsi is rather close to A. (G.) denckmanni (Wedekind 1922) sensu Engel and Schouppé (1958) in size, number of septa, septal dilatation and arrangement, and structure and relative width of tabularium. However, the German species has more frequent lonsdaleoid dissepiments, so that in transverse section the minor septa are usually highly discontinuous; also it has a rather thicker and less dentate peripheral septal stereozone. In all other described European species the minor septa are much shorter and the tabularium wider.

Known localities. Ge-2 (type); Be-7, Cr-36b, ?Ct-36.

Genus PSEUDOCHONOPHYLLUM Soshkina 1937

1937 *Pseudochonophyllum* Soshkina, pp. 59–60, 96 (*partim?*); remaining synonymy as for species.

Type species. Chonophyllum pseudohelianthoides Sherzer 1892, p. 275, pl. 8, fig. 6; designated Soshkina 1937, p. 59. Type locality: Koněprusy, Bohemia; Lower Devonian.

Diagnosis. Trochoid to cylindrical rugosan with an everted calice. Septa trabecular, the trabeculae arranged in half-fans in the wide dissepimentarium. Septa strongly dilated in dissepimentarium, generally to contact, and peripherally partly replaced by more or less well-developed naotic plates. Septa flanged in narrow tabularium. Tabularium of incomplete tabulae arranged in concave floors, frequently depressed axially.

Discussion. Počta (in Barrande 1902, pp. 123–4), describing topotypic material, considered Sherzer's species to have characteristics sufficiently removed from those of *Chonophyllum* Edwards and Haime 1850 for it to be a distinct genus, but went no further. Soshkina (1937) erected the new genus *Pseudochonophyllum* with Sherzer's species as type; in the English summary (p. 96) she referred to Sherzer's original description as being a sufficient diagnosis. In the Russian text (pp. 59–60) she gives the following (my translation):

Coral solitary, now and then giving off buds. External form subcylindrical, frequently turbinate or mushroom-shaped. Calice small, goblet-shaped, with very wide top and weak basal boss. Septal apparatus constructed of stout lamellar septa of 2 orders. These are peripherally strongly thickened with stereoplasm, and towards the axis become very thin and sometimes curved; subsequently some of them again are a little thickened at the immediate centre. Each vertical lamellar septum consists of curved roof-like platelets, superimposed one on another. Interseptal apparatus in the peripheral zone consists of numerous lamellae in the form of small vesicles. In the central zone are developed numerous very thin, strongly vesicular incomplete and confused tabulae.

Distinguished from the genus *Chonophyllum* by its pleomorphic structure and the development of 2 orders of septa. At the same time, they are similar in: 1) external form, 2) form of calice, 3) roof-shaped axial boss of complicated incomplete tabulae.

Since this paper, Soshkina has several times referred Russian species to the type species which in fact differ markedly from it, and are closer to *Acanthophyllum*. This has been recently recognized by Bulvanker (1958, p. 95), who considers Soshkina's

species to be *Acanthophylhum*, but apparently without explicitly committing herself on the Bohemian type species. She does, however, place *Pseudochonophylhum* in the synonymy of *Acanthophylhum*. She also points out the further confusion arising from Soshkina (1952, p. 98) naming as type species *P. pseudohelianthoides* Soshkina *non* Sherzer. Spasskiy (1960, p. 43) places Soshkina's species in synonymy with *Acanthophyllum heterophylhum* (Edwards and Haime 1851), but Birenheide (1963, pp. 407, 409) considers it to be a species of *Dohnophyllum* Wedekind 1923. I agree with this, and also with Birenheide's specific exclusion of Sherzer's species.

Professor E. C. Stumm has kindly sent me photographs of sections he has recently had made of the holotype of *P. pseudohelianthoides*. From this, and from the descriptions and figures given by Sherzer (1892) and Počta (in Barrande 1902) of material from the type locality, I consider *Pseudochonophyllum* to be closely related to *Acanthophyllum* and *Dohmophyllum*. It differs from the former essentially in having a reflexed calice, in having septa composed of more than one radial series of trabeculae, and in the naotic modification of the peripheral parts of the septa. *Dohmophyllum* has flat to domed tabular floors, and septa whose greatest dilatation is near the tabularium; however, the multitrabecular structure of the peripheral parts of the septa in *Dohmophyllum* (Birenheide, 1963, p. 372: text-fig. 3) is identical with the structure of the dilated portions of the septa in *Pseudochonophyllum*. The dissepimentarium and the arrangement of the septa in *Pseudochonophyllum* are typically acanthophylloid.

Of the Russian material, only that figured by Soshkina (1937, pl. 18, figs. 1–4) from the Coblenzian of the Urals probably belongs to the genus.

Pseudochonophyllum pseudohelianthoides (Sherzer 1892)

Plate 87, figs. 6-8, Plate 88, figs. 1-3

- 1892 *Chonophyllum pseudohelianthoides* Sherzer, p. 275, pl. 8, fig. 6. Koněprusy, Bohemia; Lower Devonian.
- 1902 Chonophylhun pseudohelianthoides Sherzer; Počta, p. 123, pls. 47, 48, 109 (figs. 3–6), 113 (figs. 21, 22), in Barrande. Same locality.
- ?1937 Pseudochonophyllum pseudohelianthoides Scherzer (sic); Soshkina, p. 60, pl. 18, figs. 1–4. Urals; Coblenzian.
- 1940c Acanthophyllum sp. cf. mansfieldense (Dun); Hill, p. 152, pl. 2, figs. 1a, b. Silverwood, Qld.; Couvinian?
- non 1949 Pseudochonophyllum pseudohelianthoides (Scherzer); Soshkina, p. 119, pl. 27, figs. 1, 2, pl. 28, figs. 2–5, pl. 29, figs. 2–5. Urals; $D_1^2 D_2^1$.
- non 1950 Chonophyllum pseudohelianthoides Sherzer; Termier and Termier, p. 99, pl. 39, figs. 23, 24. Morocco, N. Africa; Emsian.
- non 1952 Pseudochonophyllum pseudohelianthoides Soshkina non Sherzer; Soshkina, p. 98, pl. 38. Urals and Armenia; Coblenzian and Eifelian. (The specimen figured is Acanthophyllum.)
- non 1955 Pseudochonophyllum pseudohelianthoides Scherzer (sic); Krayevskaya, p. 218, pl. 42, figs. 4a, b, in Khalfin. W. Siberia; Coblenzian to Eifelian.
- non? 1955 Pseudochonophyllum pseudohelianthoides Soshkina; Spasskiy, p. 314 (fide Bulvanker 1958, p. 95).
 - 1962 *Pseudochonophyllum pseudohelianthoides* Sherzer; Soshkina, p. 309, in Orlov. Bohemian material only (unfigured).

Holotype. The specimen figured by Sherzer (1892, pl. 8, fig. 6) from the Lower Devonian (F2) Koněprusy Limestone of Bohemia, now in the Rominger Collection of the Museum of Palaeontology, University of Michigan. Sections have recently been made; they are figured herein (Pl. 87, figs. 6*a*, *b*).

Diagnosis. Solitary, up to 5 cm. in diameter, with strongly reflexed calice and numerous septa which may split into parallel strands peripherally; dissepiments small, gently domed, near-horizontal except in narrow zone around tabularium, where vertical.

Description. The corallite is turbinate or trochoid, becoming irregularly cylindrical, with narrow rejuvenescence rims, and growth swellings and contractions. Sherzer recorded a maximum Dc = 5 cm.; this is also known from the Wellington specimens, which generally have Dc = 3-3.5 cm. The calice is weakly to strongly everted, sometimes with a flared outer margin (the 'sattelrandiger Wulstkelch' of Birenheide 1963, p. 371, text-fig. 1). The axial pit is narrow and shallow and may have a low axial boss formed of a meshwork of septa. The septa form rounded ridges on the surface of the calice. The thin epitheca may be faintly marked by shallow interseptal grooves: unfortunately in most of the Wellington specimens it has been weathered away.

As noted also by Soshkina (1937, p. 59), and figured by Počta (pl. 47, fig. 21, in Barrande 1902), occasionally a single peripheral calical bud may occur. I have seen such small buds on 2 of the 25 or more specimens collected from the Wellington district.

Dimensions. Of representative corallites in mm.

No.		loc.	Dc	Dt	Dt/Dc	11
SU 13	180	Cr-94	32*	4.5	0.14	62
132	246	Cr-100	45*	4.5	0.10	50
132	248	,,	34*	5.0	0.15	64
	,,	,,	50*	6.0	0.12	68
132	252	,,	47	5.5	0.12	70
14	104	Cr-111	34	4.2	0.12	66
* estimated value.						

In the Wellington specimens, n = 52-68; Sherzer recorded 72. The major septa extend equally towards the axis, leaving an axial space up to 2 or 3 mm., into which septal flanges and axial processes may extend; the minor septa end just inside the tabularium. In the tabularium the septa are thin, straight, radial, and bear strong flanges; there may be some slight axial dilatation. The flanges appear in longitudinal section to be arranged in a regular zigzag pattern, and extend inwards and downwards at a low angle. In the dissepimentarium the septa are equally dilated; this increases rapidly outward from the tabularium. Within 2 or 3 mm. the septa are generally wider than the loculi, and over most of the outer half of the dissepimentarium they are in contact. An unusual feature of a number of specimens in transverse section is the apparent fusion of 2 or 3 septa to become one, as they are traced inwards from the periphery (pl. 88, fig. 3). The dilatation appears to be periodically interrupted by intervals of growth during which the septa were comparatively thin; in these intervals the septa are horizontally corrugated. This is best seen on the surfaces of weathered corallites.

In the zone of extreme dilatation the septa are frequently modified. In some instances a few septa may split into two or three parallel or anastomosing strands for a greater or lesser distance, as may occur in *Dohnophyllum* (Birenheide 1963, pl. 59, fig. 56). More often, the septa are replaced by naotic plates, supported by isolated trabeculae. These plates are small, very gently domed, radially elongate, and parallel in inclination to the dissepiments. Unlike *Craterophyllum* Foerste, the plates generally do not extend from

one side of the septum to the other in a regular manner; they overlap in a manner more like that of dissepiments, and may occasionally extend across two or three septa (see Sherzer 1892).

The septal trabeculae are up to 0.2 mm. thick; they diverge from a median plane in the septum, although that plane is not expressed morphologically; they are radially arranged in half-fans. A few millimetres outside the tabularium they are vertical; outside this, they are directed upwards and slightly outwards, until at the periphery they may again become vertical. Towards the tabularium they are directed axially upwards at an angle of about 30° from the vertical. The trabeculae in the tabularium are too fine to show whether a second fan develops there as in *Acanthophyllum* s.s.

The tabularium is narrow: Dt = circa 5 mm., and Dt = 0.12Dc approximately, being generally between 0.11 and 0.14Dc. The tabular floors are gently sagging, with slightly to strongly upturned margins; there may be a slight median depression. The tabulae are incomplete, thin, and flat to slightly convex.

The very wide dissepimentarium consists of small gently to strongly domed dissepiments. Over most of the dissepimentarium they are horizontal to slightly inclined outwardly, following the calical shape. In a narrow zone around the tabularium they are vertical and elongate. The dissepiments may be coated with thin fibrous extensions of the septal dilatation.

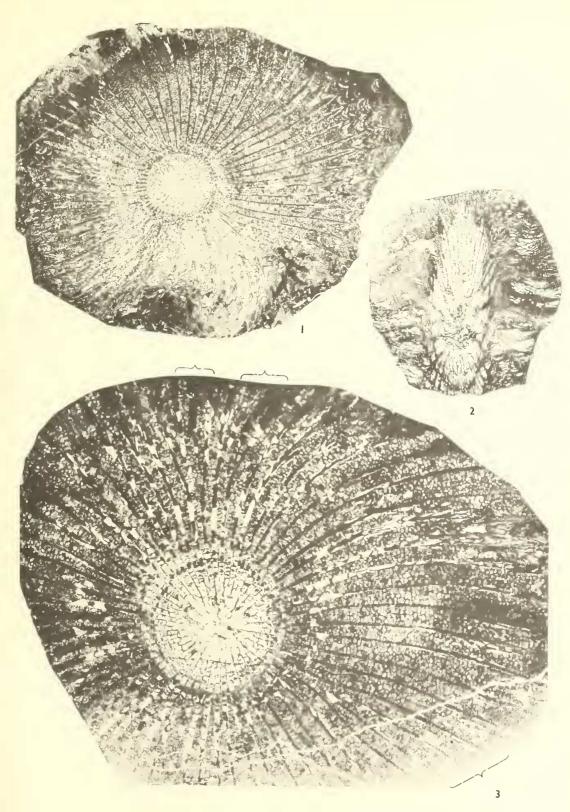
Remarks. From an examination of the photographs kindly supplied by Professor Stumm, and of the figures of Sherzer and Počta, there would seem to be very little difference between the Garra and Koněprusy material. The naotic plates in the Bohemian specimens apparently show a greater tendency to extend across two or three septa, and the dilatation of the septa does not show the periodic reduction to nearly the same extent. The only possible argument against specific identity is that, as the Russian material is excluded from the species, there is no record of it between Bohemia and Eastern Australia.

The Silverwood specimen described by Hill (1940c) as *Acanthophyllum* sp. cf. *mans-fieldense* has all the features of the present species—extreme septal dilatation consisting of thick trabeculae, peripheral naotic modification, reflexed calice—and I consider it to be specifically identical with the present species. It is figured herein for comparison (pl. 87, fig. 8*a*, *b*).

Range. The Koneprusy Limestone is considered to be time-transgressive, extending through the whole of the Lower Devonian (see, e.g. Havlíček 1959). Hill (1940*c*) considered the Silverwood fauna to be probably Lower Couvinian, and equivalent to the Nemingha fauna of Tamworth. I consider both these, and the Garra Formation, to be more likely Emsian in age (see Strusz 1965); this would be supported by correlation with Koněprusy.

EXPLANATION OF PLATE 88

Figs. 1–3. *Pseudochonophyllum pseudohelianthoides* (Sherzer 1892). 1, transverse section showing septa at various degrees of dilatation; SU 13248, loc. Cr–100; $\times 2$. 2, oblique longitudinal section showing acanthophylloid tabularium, and septal flanges; SU 13249, loc. Cr–100; $\times 2$. 3, transverse section showing details of septal structure; 'fused' septa are bracketed peripherally (see p. 565); SU 13248, loc. Cr–100; $\times 4$.



STRUSZ, Devonian Spongophyllidae from New South Wales



Known Garra localities. All specimens have been collected from three localities in a biostrome cropping out in the generally massive limestones on the west bank of the Bell River, opposite the Wellington Caves Reserve: Cr–94, Cr–100 (common), Cr–111.

Genus LYRIELASMA Hill 1939

1925 *Cyathophyllum (partim)* Chapman, p. 112. 1939a *Lyrielasma* Hill, p. 243.

Type species. Cyathophyllum subcaespitosum Chapman 1925, p. 112, pl. 13, figs. 15, 16*a*, *b*. Cave Hill Lilydale, Vic:; Siegenian ?—Philip 1960, p. 151.

Diagnosis. As *Acanthophyllum*, but fasciculate to subcerioid; calice inversely conical; with wide peripheral stereozone.

Discussion. Corallites of *Lyrielasma* are narrow, cylindrical, with an inversely conical calice (the 'trichterkelch' of Wedekind—see Birenheide 1961). There is usually a relatively wide peripheral stereozone formed by the dilatation of the septal bases; this is widest in the type species, and narrowest in '*Grypophyllum*' aggregatum Hill 1940. In some cases this stereozone is partly broken up by lonsdaleoid dissepiments. The characters of the dissepimentarium and tabularium are much as in *Acanthophyllum* (*Grypophyllum*).

Grypophyllum aggregatum Hill 1940b, from the Eifelian? of the Murrumbidgee River, is a phaceloid species, and so is here removed from *Grypophyllum*, which Birenheide (1961, p. 114) has shown to be solitary, to *Lyrielasma* (see pp. 570–1).

Lyrielasma curvatum Hill 1942a (p. 238), from the Givetian Fanning River Limestone, differs from the type species in having flat to domed tabular floors. It is more akin to Grypophyllum compactum Hill 1942 (p. 255) and G. sp. Hill 1942 (p. 255), from the same formation, none of these species being either Lyrielasma or Grypophyllum.

Lyrielasma? micrum sp. nov.

Plate 89, figs. 1, 2; text-fig. 8

Derivation of name. Greek $\mu \kappa \rho os = small$.

Holotype. SU 18200 (Pl. 89, fig. 1a, b). Type locality: P-43.

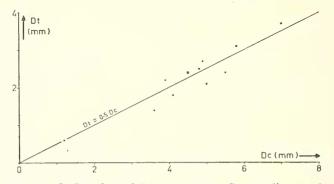
Diagnosis. Lyrielasma about 5–6 mm. in diameter with relatively wide peripheral stereozone and zigzag septa, and lacking lonsdaleoid dissepiments; calice deeply conical.

Description. The form of the corallum is unknown, as all specimens are of fragmentary cylindrical corallites; however, the holotype shows evidence of a dendroid growth form, with lateral increase. The epitheca is thin, longitudinally and transversely wrinkled, but without regular septal grooves. Narrow, sharp rejuvenescence rims occur (holotype, and SU 18195). Longitudinal sections suggest a very deep calice, inversely conical in shape, with a sharp or slightly rounded rim and a narrow concave base. Maximum Dc = 7 mm., normal adults being 4–6 mm. across.

Dimensions. In mm. of representative corallites.

No.	loc.	Dc	Dt	Dt/Dc	11	L_2
SU 16299	Gg-2	4.9	2.7	0.55	32	0.3 R
SU 18195	P-43	7.0	3.7	0.53	38	0·4–0·7 R
SU 18200*	,,	1.2	0.6	0.50	12	
,,	,,	4.5	2.4	0.53	36	0.4 R
,,	>>	5.0	2.1	0.42		
* Holotype						

Lining the thin epitheca is a relatively wide stereozone composed of dilated septal bases, which in some instances apparently merge into lamellar sclerenchyme parallel to the epitheca. This last may, however, be an effect of recrystallization. The stereozone is 0.5-1.0 mm, wide. In adults, n = 30-40; the major septa extend unequally to the axis,



TEXT-FIG. 8. Lyrielasma? micrum sp. nov. Scatter diagram for Dt:Dc; the estimated approximate mean, Dt = 0.5Dc, is added.

where they are curved and arranged about a median plane. One major septum (K?) may be elongate, extending across the axis. The minor septa vary in length from 0.3R to 0.7R, being generally about 0.5R. Inside the stereozone the septa are equally and moderately dilated, irregularly wavy, and bear zigzag flanges which are inclined steeply down towards the axis.

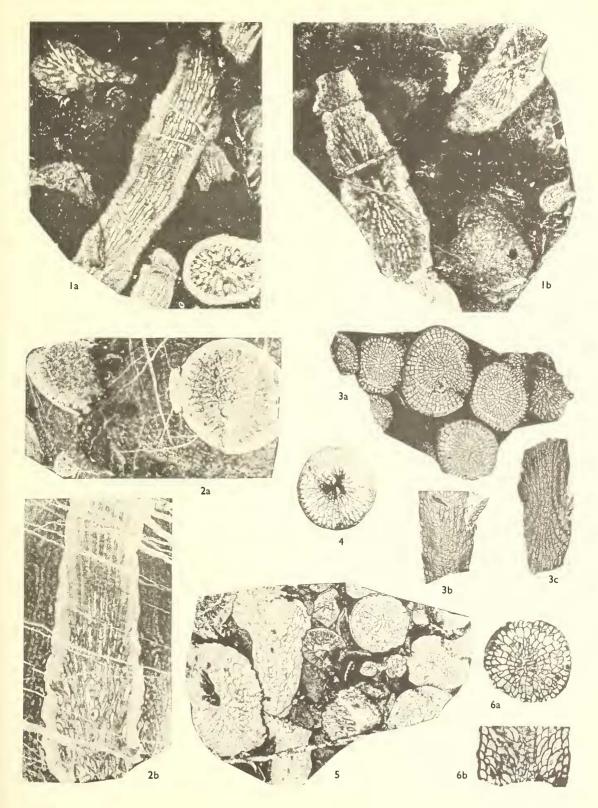
The trabeculae are very narrow and are approximately parallel throughout their length. The structure of the trabeculae is much as described by Birenheide (1961) for *Acanthophyllum*. They are directed axially upwards at a very small angle above the horizontal.

Dt = 0.5Dc approximately (see text-fig. 8), ranging between 0.39-0.56. The tabular

EXPLANATION OF PLATE 89

Figs. 1, 2. *Lyrielasma? micrum* sp. nov. 1*a*, *b*, transverse and longitudinal sections, holotype SU 18200, loc. P–43; ×4. 2*a*, transverse section showing wide stereozone, thick septa, 2*b*, longitudinal section; SU 18195, loc. P–43; ×4.

^{Figs. 3–6. Lyrielasma aggregatum (Hill 1940). 3a–c. transverse and longitudinal sections, holotype AM F 10132, Wee Jasper, near Taemas, N.S.W.; figured Hill 1940b; × 2. Photographs by courtesy of the Australian Museum, Sydney. 4, transverse section at base of calice, SU 19147, loc. St/1821; × 2. 5, random section through a fragmented colony, UCT F 1946, The Gap (loc. E–18?); × 2. 6a, b, transverse and longitudinal sections, SU 14257, loc. Ct–50; × 2.}



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floors are deeply inversely conical, with a narrow concave base, but a median depression has not been seen. The tabulae are incomplete, steeply inclined, elongate, and but little inflated.

The disseptimentarium consists of 2–4 series of almost vertical fairly elongate to moderately globose disseptiments, generally uniform in size.

Comparison. L? micrum differs from all other Australian species of *Lyrielasma* in its small size and proportionately wide stereozone. The type species is closest in appearance, differing essentially in size and number of septa.

Remarks. Because of the slight doubt whether this species is colonial or not, it is for the present only tentatively assigned to *Lyrielasma*.

Known localities. Gg-2, P-43; BR¹/177.

Lyrielasma subcaespitosum (Chapman 1925)

1962 Lyrielasma subcaespitosum (Chapman); Philip, p. 188, pl. 28, figs. 6-7. Cum Syn.

Holotype. NM 1731, 14065: Cave Hill, Lilydale. Figured Hill (1939a), pl. XIV, figs. 1–3.

Diagnosis. Phaceloid *Lyrielasma* about 12 mm. in diameter, with long wavy to zigzag or flanged septa seldom interrupted by lonsdaleoid dissepiments.

Remarks. L. subcaespitosum praecursor Philip 1962 (p. 119) differs from *L. subcaespitosum* s.s. in being wider, with a wider stereozone, wide tabularium ($Dt = \frac{1}{2}Dc$), and frequent lonsdaleoid dissepiments, interrupting both major and minor septa. The specimens described below have features in common with both subspecies.

Lyrielasma sp. cf. subcaespitosum

Plate 87, fig. 5

Material. SU 12245 (loc. Cr-4)?; SU 19238 (Pl. 87, fig. 5), 19241 (loc. St/2565).

Description. The material consists of fragmentary corallites; it is not known whether or not they are from fasciculate coralla. The external characters are unknown.

Dimensions. In mm.

No.	Dc	Dt	Dt/Dc	11
SU 12245	est. 10	est. 4.5	ca. 0·45	60?
SU 19238	est. 9	5.5	<i>ca</i> . 0.6	46

The corallites are about 10 mm. in diameter. There is a peripheral stereozone about 0.7 mm, wide, formed of the dilated ends of septa. Inside this the septa suddenly reduce in thickness, and maintain a fairly uniform moderate dilatation to the axis. Irregular flanges occur in both dissepimentarium and tabularium.

The major septa extend unequally to the axis, being directed towards a median plane which in SU 19238 is marked by one long and one short major septa. n = about 50-60. The minor septa vary considerably in length between $\frac{1}{4}R$ and $\frac{1}{2}R$, being mostly about R/3. Septal microstructure is not clear in the available material. Dt = *circa* 0.5 to 0.6 Dc. The tabular form is not known. The rather narrow dissepimentarium is not well known; for the most part it is masked by the peripheral stereozone and the septal dilatation.

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It apparently consists of small, highly inclined dissepiments. I have seen no lonsdaleoid dissepiments.

Remarks. The available material differs from *L. subcaespitosum* s.s. in its wider tabularium, and possibly in having smaller dissepiments. From *L. subcaespitosum praecursor* Philip 1962, which also has a wide tabularium, the specimens differ in lacking all sign of lonsdaleoid dissepiments, and in having a narrower stereozone.

Lyrielasma aggregatum (Hill 1940)

Plate 89, figs. 3-6, Plate 90, fig. 1; text-figs. 9, 10

- 1940b Grypophyllum aggregatum Hill, p. 268, pl. X, figs. 8a, b, pl. XI, figs. 1a-d. Wee Jasper, N.S.W.; Eifelian.
- 1942*d* ?*Grypophyllum* ?*aggregatum* Hill; Hill, pl. VI, fig. 4. Wellington, N.S.W.; 'Early Couvinian' (probably Emsian).

Holotype. AM F 10132, Wee Jasper, Goodradigbee R., N.S.W., figured Hill (1940b) pl. XI, figs. 1*a*–*d*; figured herein Plate 89, figs. 3 *a*–*c*.

Diagnosis. Lyrielasma with thin septa, narrow stereozone, wide tabularium, and absent or rare lonsdaleoid dissepiments.

Description of Garra material. Available material is more or less fragmentary, but UCT F 1946 shows evidence of a dendroid corallum in which increase is both sexual (planulae settling on the sides of existing corallites) and by peripheral budding. The latter apparently produces only one bud at a time and is non-parricidal. The epitheca is smooth, or marked with faint longitudinal grooves which show little relationship to the septa; it is thin. The calice is uncertain; longitudinal sections suggest a deeply inversely conical calice with a narrow rounded rim. The maximum observed Dc = 11.8 mm.; adults are normally about 5–9 mm. across.

Dimensions. In mm. of representative corallites.

No.	loc.	Dc	Dt	Dt/Dc	п	L_2	stereozone
SU 14257	Ct-50	11.8	ca.0.5	ca.0.42	50	0·20·4 R	0.5 mm.
UCT F 1946	'The Gap'	2.9	1.7	0.59	26	0·10·2 R	0.1
,,	>>	4.3	3.6	0.84	30	0·1-0·3 R	0.3
>>	,,	6.5	3.2	0.49	38	0·3–0·4 R	0.6
>>	,,	8.8	4.2	0·48	38	0·3–0·5 R	0.4
SU 19147	St/1821	10.1	4.5	0·45	44	0·3–0·8 R	0.4

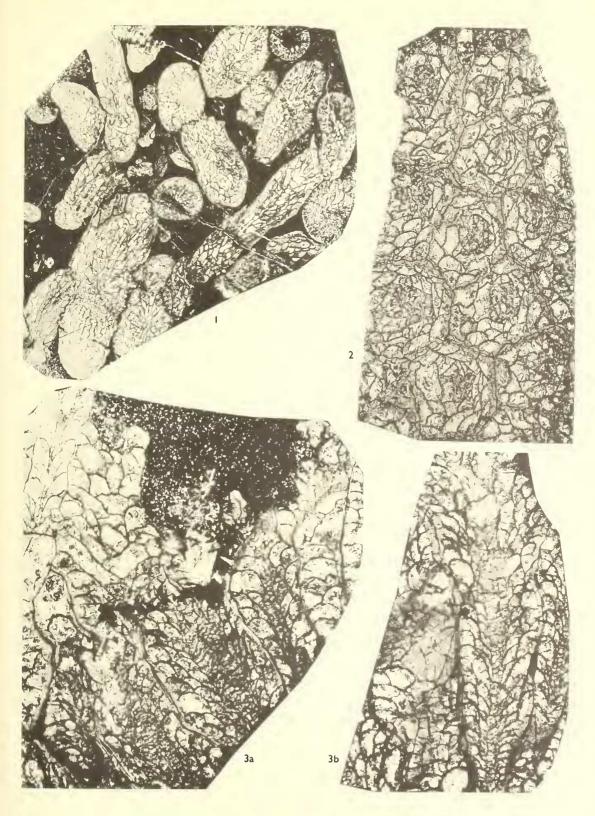
Maximum observed n = 50; for normal adults n = 34-44, mostly 38 or 40. The major septa extend unequally towards a median plane, and generally leave a small axial space. The minor septa are considerably more variable in length, even in the same corallite, ranging between 0.1-0.8 R; they are usually 0.3-0.5 R. The septa are equally dilated; their bases are flared to form a peripheral stereozone 0.5 mm. wide at

EXPLANATION OF PLATE 90

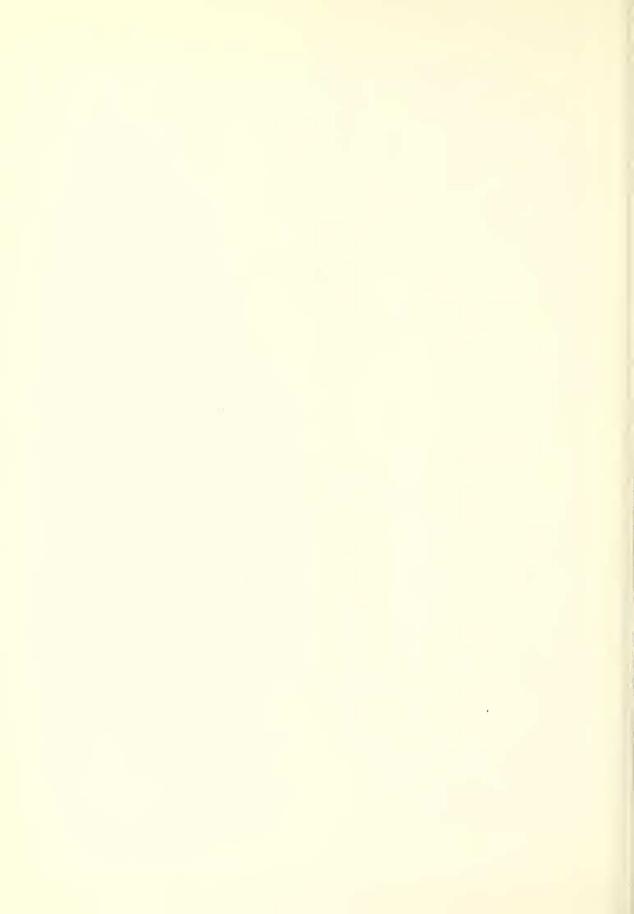
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Fig. 1. Lyrielasma aggregatum (Hill 1940). Random section through a fragmented colony; note the peripheral buds in the longitudinal section of a large corallite, lower left; UCT F 1946, The Gap (loc. E-18?); ×2.

FIGS. 2, 3. Spongophyllum halysitoides halysitoides Etheridge fil. 1918. 2, transverse section, SU 16224, loc. E-30; ×4. 3a, b, longitudinal sections, SU 16223, loc. E-30; ×4.



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most. Inside this they are tapered, generally only moderately to slightly dilated, and frequently attenuate in the tabularium. They are zigzag, and occasionally bear weak flanges; their inner ends may be curved. In SU 14257 the minor septa are contratingent, and thus indicate the median plane: at one end they lean away from the major septum (C?), and they continue leaning in that sense until at the other end the one major septum (K?) has two touching minor septa. Generally, however, the minor septa are far less regular.

Dt = 0.5Dc approximately. The tabularium consists of elongate, highly inclined, slightly convex incomplete tabulae, forming moderately to strongly inverse conical tabular floors.

There are from one to four series of globose highly inclined dissepiments which tend to become vertical and rather elongate near the tabularium. Lonsdaleoid dissepiments are rare, and when present only intersect the minor septa. I have seen them in SU 5280 (collected E. M. Basnett 1940, from loc. MM–10) and in two corallites from loc. Ct–50.

Variation. Plots have been made for Dt: Dc, Dt/Dc: Dc, and n: Dc. The estimated curve of best fit for the first approximates to Dt = 0.5Dc. The points fall slightly above this line between Dc = 0 and 8.0 mm., and then slightly below it for greater Dc (text-fig. 9*a*). This is shown more accurately by the plot Dt/Dc: Dc (text-fig. 9*b*); at Dc = 3 mm., Dt/Dc is about 0.55; at Dc = 8 mm., Dt/Dc = 0.50; and at Dc = 11 mm., Dt/Dc has fallen to about 0.45.

The number of septa apparently increases rapidly at first (text-fig. 10), as at Dc = 2.9 mm. (the smallest measurement), n = 26. Beyond this, however, the relationship of n:Dc is linear, approximating to n = 20+2.5Dc.

In no cases is the scatter of points excessive.

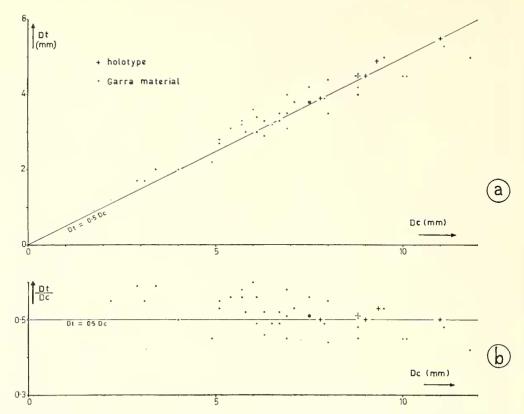
Comparison. L. aggregatum differs from *L. subcaespitosum* s.s. in a smaller average size, a narrow stereozone, and thinner septa. From *L. subcaespitosum praecursor* Philip 1962 it differs especially in the general lack of lonsdaleoid dissepiments, and also in size and width of stereozone. From *L. floriforme* Hill 1942 it differs in size, width of stereozone, and in having tapered rather than fusiform septa; *L. aggregatum* also has a wider tabularium. *L. lophophylloides* Hill 1942 is very similar; it is distinguished by having four prominent, longer and thicker major septa, and a narrower tabularium.

Remarks. Hill (1940b, p. 268) placed this species in *Grypophyllum* because at that time she considered that that genus included phaceloid species. However, she also drew attention to the similarity of the species to *Lyrielasma*. As Birenheide (1961) has shown that *Grypophyllum* is a solitary subgenus of *Acanthophyllum*, and as 'G.' aggregatum differs from other species assigned to *Lyrielasma* essentially only in having a narrow stereozone, I have herein placed it in *Lyrielasma*.

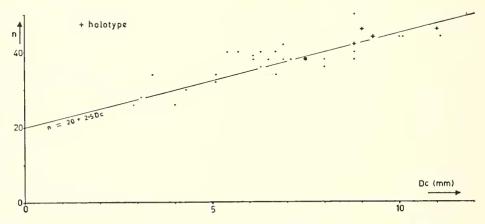
Range. The species has been recorded from the Murrumbidgee limestones (Couvinian according to Hill 1940*b*, p. 249; Emsian according to Philip and Pedder 1964), and from the Garra Formation (which I consider to be probably Emsian). It has also been found at Douglas Creek, Clermont, Qld. (UQ F 36328), considered by Hill (1939*b*) to be probably upper Couvinian in age.

Known Garra localities. Ct–50, MM–10, MM–12; St/181, St/1125, St/1821; also collected by Dr. J. Conolly from 'The Gap', probably loc. E–18.

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TEXT-FIG. 9. Lyrielasma aggregatum. Scatter diagrams for (a) Dt:Dc, and (b) Dt/Dc:Dc, with data for the holotype added (measured from published photographs); for comparison, the line Dt = 0.5Dc is added.



TEXT-FIG. 10. Lyrielasma aggregatum. Scatter diagram for n:Dc, with data for the holotype added; the estimated approximate mean n = 20+2.5Dc is also added.

Genus SPONGOPHYLLUM Edwards and Haime 1851

- 1851 Spongophyllum Edwards and Haime, p. 425 (fide Lang, Smith, and Thomas 1940, p. 121).
- 1962 *Spongophyllum* Edwards and Haime 1851; Birenheide, p. 69 (*partim*). Contains an extensive synonymy, to which add:
- 1962 Neomphyma Soshkina 1937; Soshkina and Dobrolyubova, p. 335, in Orlov (partim).

Type species. By monotypy, *S. sedgwicki* Edwards and Haime 1851, p. 425. Neotype, selected Jones (1929, p. 88), figured Birenheide (1962) pl. 9, fig. 8, pl. 10, fig. 10. Torquay, Devonshire; Middle? Devonian.

Diagnosis. Phaceloid or, more usually, cerioid, with small corallites; narrow tabularium of flat or gently concave complete tabulae; dissepimentarium of only a few series of globose lonsdaleoid dissepiments and smaller interseptal dissepiments; septa thin, poorly developed, generally based on lonsdaleoid dissepiments.

Remarks. The genus has been well revised by Jones (1929), Prantl (1952), and Birenheide (1962). Birenheide would include *Australophyllum* Stumm 1949. As proposed by Stumm, there is certainly no difference; however, the type species shows certain points which I consider sufficient to justify retention of the genus. The tabulae are concave, with a definite median depression such as typifies the acanthophylloid genera. Also the dissepimentarium is rather wide for typical *Spongophyllum*.

Spongophylhum halysitoides halysitoides Etheridge fil. 1918

Plate 90, figs. 2, 3; text-figs. 11, 12

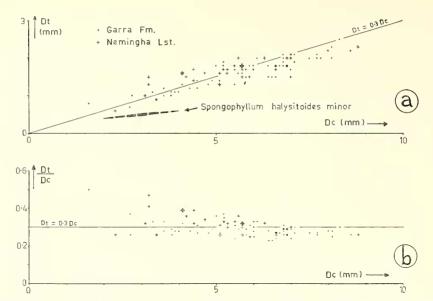
- 1918 Spongophyllum halysitoides Etheridge fil., p. 49, pl. VII. Tamworth, N.S.W.; Coblenzian.
- 1932 Spongophyllum halysitoides Etheridge fil.; Jones, p. 56 (partim—not text-fig. 2). Tamworth.
- 1942c Spongophyllum halysitoides Etheridge; Hill, p. 161, pl. II, figs. 5a, b. Tamworth.
- non 1958 Spongophyllum halisitoides (sic) Etheridge; Bulvanker, p. 132, pl. LXIV, figs. 1a, b, 2. Kuznets Basin, U.S.S.R.; lower Eifelian.
 - 21960 *Spongophyllum halysitoides* Etheridge; Spasskiy, p. 55, pl. XXIX, figs. 3, 4. Altai, U.S.S.R.; lower Middle Devonian.

Holotype. AM F 16453 (AM 187), figured Etheridge, jr. 1918, pl. VII, figs. 1–3. Type locality: road near Beedle's Farm, Moonbi, Co. Inglis, Tamworth, N.S.W. Nemingha Limestone, Coblenzian.

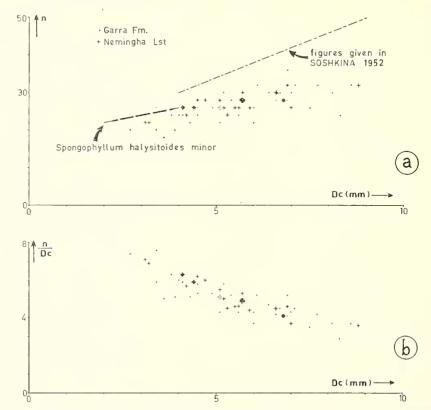
Diagnosis. Cerioid *Spongophyllum* with corallites mostly 4–6 mm. in diameter, with thick moniliform walls; septa much reduced or absent; tabularium narrow.

Remarks. The specimens from the Garra Formation agree closely with the descriptions and figures of Etheridge, jr. (1918) and Jones (1932). The only differences lie in a slightly stronger and more frequent development of septa, and in thicker walls. Some of the Garra specimens have noticeably irregular corallites.

The Garra material has been statistically compared with a specimen I have collected from the Nemingha Limestone in a quarry just north of Attunga (near Tamworth), and with SU 6241 from the same horizon at Por. 256, Ph. Burdekin, near Tamworth. The Tamworth and Garra specimens agree completely (text-figs. 11, 12). The range of variation is greater than stated by Etheridge, the maximum diameter being nearly 9 mm.; most corallites are about $3 \cdot 5-7$ mm. across. For both, Dt = $0 \cdot 3Dc$ approximately, and Dt/Dc seems to decrease only slightly with increasing Dc. A plot of n/Dc:Dc suggests a slight change in rate of septal insertion with age.



TEXT-FIG. 11. Spongophyllum halysitoides halysitoides. Scatter diagrams for (a) Dt: Dc, and (b) Dt/Dc: Dc; data from specimens from the Garra Formation and the Nemingha Limestone (the type horizon). The estimated approximate mean line Dt = 0.3Dc is shown, and also in (a) the range of values for *S. halysitoides univor* (from the figures given by Hill).



TEXT-FIG. 12. Spongophyllum halysitoides. Scatter diagrams for (a) n:Dc, and (b) n/Dc:Dc for S. halysitoides halysitoides from the Garra Formation and the Nemingha Limestone. In (a) the range of values given by Soshkina (1952), and for S. halysitoides minor by Hill (1940c) are also shown.

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'Varieties' of *S. halysitoides* have been established by both Hill (1940*c*) and Soshkina (1949), distinguished principally on corallite size. I consider that their geographic separation, taken with the morphological differences, suffice for these to be subspecies. Etheridge jr.'s original species is a distinct subspecies. *S. halysitoides minor* Hill 1940 is diminutive (Dc = 2-4 mm.), with a very narrow tabularium; from the figures given by Hill, its range of variation for Dt:Dc falls below the area of scatter for the nominate subspecies. It is known from the Coblenzian? of Silverwood, Qld., and the Urals. *S. halysitoides media* Soshkina 1949, from the Eifelian of the Urals, is close to, indeed may be synonymous with, the nominate subspecies (Dc = 5-6 mm.), but has better developed septa. The size range, and number of septa, given for the species by Soshkina (1952)—probably based on the Russian material—falls well above the scatter area for n:Dc for *S. halysitoides halysitoides* (text-fig. 12), suggesting that the Russian material may differ in this respect also. *S. halysitoides major* Soshkina 1949, also from the Eifelian of the Urals, is large (Dc = 8-9 mm.), with well-developed septa; it should perhaps be considered a separate species.

The specimen figured by Bulvanker (1958, pl. 64) from the Eifelian of the Kuznets Basin has very well-developed septa—in fact in most corallites they appear to be continuous—as well as smaller disseptments and distinctly acanthophylloid tabulae. It is probably a species of either *Australophyllum* or *Xystriphyllum*.

Range. The species is known from the Coblenzian of Eastern Australia, and the Coblenzian and Eifelian of the U.S.S.R. The nominate subspecies is known only from the Coblenzian.

Known Garra localities. Ct-29?, E-24, E-30, E-31; Bt/430, Bt/936.

Spongophyllum rosiforme Yoh 1937

1937 Spongophyllum rosiforme Yoh, p. 54, pl. VI, figs. 1*a–c*. Kwangsi, China; middle Middle Devonian.

Diagnosis. Phaceloid *Spongophyllum* with corallites about 9 mm. in diameter, buttressed by lateral expansions; septa few, irregular, confined to tabularium; one peripheral series of large geniculate dissepiments, supplemented axially by intermittent small, vertical elongate dissepiments; tabularium narrow, of close, gently concave tabulae.

Spongophyllum sp. cf. rosiforme Yoh 1937

Plate 91, figs. 1a, b; text-fig. 13

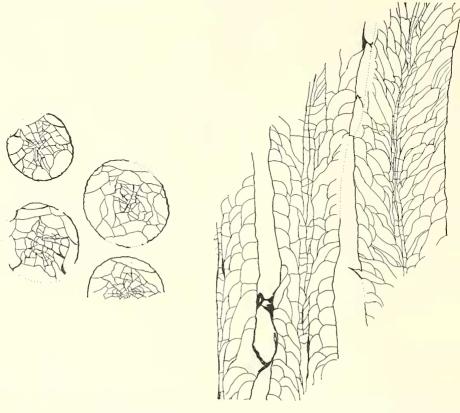
Material. SU 17167, loc. P-1.

Description. The corallum is phaceloid, composed of cylindrical corallites with frequent lateral processes. The epitheca is apparently smooth, with gentle growth swellings. The calice is deep, inversely conical to bell-shaped. Dc = 6-8 mm.

The septa, consisting of discontinuous crests on the dissepimental surfaces, are unequal and not divisible into two orders. n = 14-16 in general. Most are confined to the tabularium but exceptionally they may extend outwards as far as the epitheca. The longest septa often interfinger axially. The thin epitheca is lined by a lamellar stereozone 0.2 mm. thick, in which septal bases are not visible. Septal microstructure is unknown.

 $Dt = \frac{1}{4}Dc$ or less. The tabulae are close, and gently but irregularly sagging, at times with upturned edges.

The wide dissepimentarium consists of a peripheral series of large globose to geniculate lonsdaleoid dissepiments, and an incomplete inner series of very elongate,



TEXT-FIG. 13. Spongophyllum sp. cf. rosiforme. Transverse and longitudinal sections of SU 17167, ×3; drawn from photographs.

steeply inclined dissepiments, some of them lonsdaleoid, which may be supplemented by occasional small convex plates.

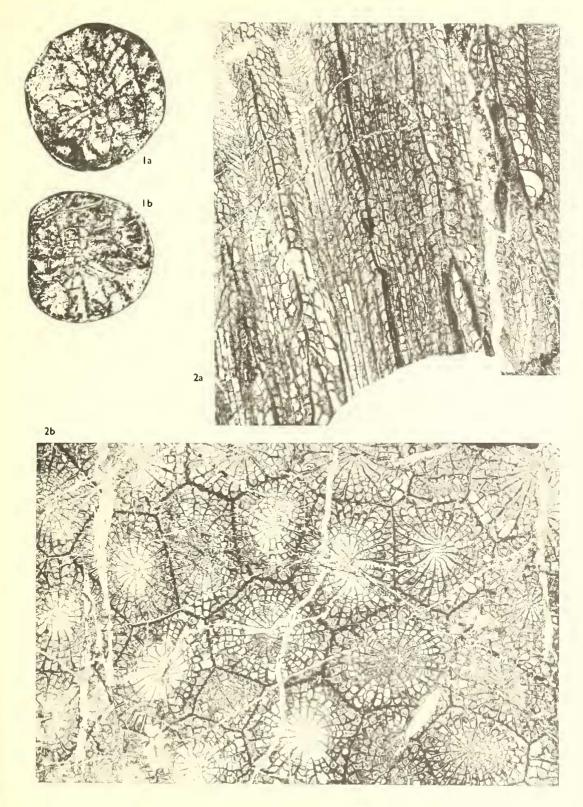
Comparison. This specimen differs from Yoh's only in a slightly smaller diameter, and 14–16 instead of 20 septa. The differences could be of subspecific value, but as the possible variation in both cases is unknown, I consider it best for the present simply to compare them.

All figures $\times 4$.

EXPLANATION OF PLATE 91

Fig. 1. Spongophyllum sp. cf. rosiforme Yoh 1937. 1a, b, transverse sections of individual corallites (cf. text-fig. 13), SU 17167, loc. P-1.

Fig. 2. *Xystriphyllum dunstani* (Etheridge fil. 1911). 2*a*, *b*, longitudinal and transverse sections, paralectotype AM F 9492–3, AM 733 A, B, Clermont, Qld. Photographs by courtesy of the Australian Museum, Sydney.



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Genus XYSTRIPHYLLUM Hill 1939

- 1939b Xystriphyllum Hill, p. 62.
- 1940b Xystripliyllum Hill; Hill, p. 269.
- 1940c Xystriphyllum Hill; Hill, p. 163.
- 1942c Xystripliyllum Hill, 1939; Hill, p. 147.
- 1942d Xystripluyllum; Hill, p. 183.
- 1949 Xystriphyllum Hill; Stumm, p. 33.
- 1949 Stenophyllum; Soshkina, p. 127 (partim).
- 1950 Xystriphyllum Hill, 1939; Hill, p. 140.
- 1950 Xystriplyllum Hill, 1939; Wang, p. 218.
- 1952 Stenophyllum Wdkd.; Soshkina, p. 83 (partim).
- ?1955 Pseudospongophyllum Zhmaev; Krayevskaya, p. 213, in Khalfin (partim?).
- 1955 Stenophyllum Amanshauser, em. Wedekind; Krayevskaya, p. 211, in Khalfin (partin).
- ?1955 Spongophyllum M. Edwards et Haime; Krayevskaya, p. 214, in Khalfin (partim?).
- 1956 Xystriphyllum Hill; Clauss, p. 16.
- 1956 Xystriphyllum Hill, 1939; Hill, p. F304, in Moore.
- 1958 Stenophyllum (Amanshauser) emend. Wedekind, 1925; Bulvanker, p. 146 (partin).
- non 1960 Xystriphyllum Hill; Crickmay, p. 11.
 - ?1961 Xystriphyllum Hill 1939; Fontaine, p. 158 (partim?).
 - 1962 *Xystriplyllum* Hill 1939; Philip, p. 188.
 - 1962 Xystriphyllum Hill, 1939; Soshkina and Dobrolyubova, p. 335, in Orlov.

Type species. Cyathophyllum dunstani Etheridge fil. 1911, p. 3, pl. A, figs. 1, 2 (see below).

Diagnosis. Cerioid; septa long, wavy, thin axially, dilated peripherally; tabulae close, complete or incomplete, concave with axial depression; dissepiments globose, axially inclined, becoming steep at margin of tabularium; minor septa occasionally cut by lonsdaleoid dissepiments.

Remarks. Many of the Russian species assigned to *Stenophyllum* Wedekind (*non* Verhoeff 1897) are *Xystriphyllum*; others are *Acanthophyllum* s.1. I would place the following in *Xystriphyllum: Stenophyllum* altum Soshkina 1949, p. 128 (Eifelian, Urals); *S. uralicum* Soshkina 1949, p. 129 (Eifelian, Urals); *S. gorskii* Bulvanker in Krayevskaya, 1955, p. 211, in Khalfin (Coblenzian, Kuznets Basin, Central Salair; Eifelian, Kuznets Basin—Bulvanker 1958); this probably is synonymous with *X. dunstani*, which see; *S. sibiricum* Bulvanker in Krayevskaya 1955, p. 211, in Khalfin (Eifelian, Kuznets Basin); *S. devonicum* Bulvanker in Krayevskaya 1955, p. 211, in Khalfin (Eifelian, W. Siberia, Kuznets Basin, and Altai mineral field); *S. salairicum* Zhmaev in Krayevskaya 1955, p. 212, in Khalfin (Eifelian, Kuznets Basin); *S. soshkinae* Zhmaev in Krayevskaya 1955, p. 40 (Emsian, central Taimyr).

The following may also belong in *Xystriphyllum: Spongophyllum minimum* Zhmaev in Krayevskaya 1955, p. 215, in Khalfin (Lower Devonian, Salair); *Psendospongophyllum massiyum* Zhmaev in Krayevskaya 1955, p. 213, in Khalfin (Eifelian, Kuznets Basin); *Spongophyllum halysitoides* Etheridge of Bulvanker 1958, p. 132 (*non* Etheridge jr. 1918) (Lower Eifelian, Kuznets Basin).

Range. The genus is known from the Lower Devonian of America and Czechoslovakia, the upper Lower to basal Middle Devonian of Australia, the Coblenzian to Eifelian of the U.S.S.R., the Couvinian of Laos?, and the Frasnian of Menorca.

Xystriphyllum dunstani (Etheridge fil. 1911)

Plate 91, fig. 2, Plate 92; text-figs. 14-17

- 1911 Cyathophyllum dunstani Etheridge fil., p. 3, pl. A.
- non 1935 ?Cyathophyllum dunstani Etheridge; Allan, p. 6, pl. V, figs. 4, 5. Reefton, N. Zealand; Eifelian?
 - 1939*b* Xystriphyllum dunstani (Etheridge); Hill, p. 62, pl. V, figs. 5–8. Clermont, Qld.; Eifelian?
 - 1940c Xystriphyllnm dunstani (Etheridge); Hill, p. 163, pl. III, figs. 4a, b. Silverwood, Qld.; Eifelian?
 - 1942*d Xystriphyllum dunstani* (Etheridge); Hill, pp. 183, 184, pl. VI, figs. 2*a*, *b*. Wellington, N.S.W.; Emsian?
 - 21955 Stenophyllum gorskii Bulvanker in Krayevskaya, p. 211, pl. XXXVII, fig. 2, in Khalfin. Kuznets Basin and Central Salair, U.S.S.R.; Coblenzian.
 - ?1958 Stenophylhum gorskii Bulvanker (partim); Bulvanker, p. 147, pl. LXXI, figs. 1a, b, 2, pl. LXXII, figs. 1a, b. Kuznets Basin, U.S.S.R.; Eifelian.

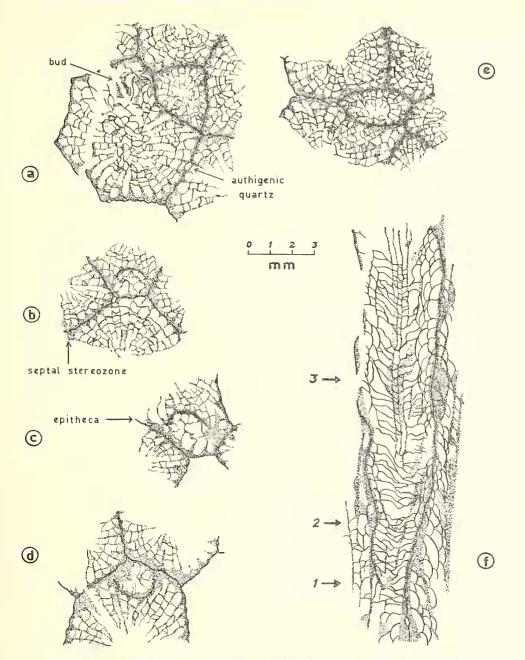
Lectotype. GSQ Cl.6; subsequent designation Hill (1939b) p. 62, where figured plate V, figs. 5–8. Type locality: Douglas Ck., Clermont, near Rockhampton, Qld. Eifelian? Paralectotype AM F 9492–9493 (sections AM 733), figured Etheridge jr. (1911), pl. A, figs. 1, 2; figured herein plate 93, figs. 2*a*, *b*.

Diagnosis. Xystriphyllum with corallites of average diameter 6–8 mm., in which the major septa interdigitate axially.

Description. I have collected a large amount of material from the Garra Formation, and have compared it with the lectotype, and with other material in the collections of the University of Queensland, the University of Sydney, and the Australian Museum. The following description is based on all of this, but principally on the extensive Garra material.

The corallum is massive and may reach a large size. Thus SU 17184 (loc. P-22) is 30 cm. high and over 30 cm. across, and is part of a non-radiating corallum. The holotheca is unknown. Calices are deep, conical to slightly bell-shaped, with steep, straight to moderately convex walls, narrow rims, and narrow concave bases. Individual corallites are 4- to 8-sided, generally with straight or slightly crenulate walls. The majority of adult corallites are 6-8 mm. in diameter (see text-fig. 15*a*). The corallite epitheca is longitudinally ribbed, but shows only sparse and very faint transverse growth marks. The wall structure comprises a thin dark median surface, representing the epitheca of adjacent corallites (the 'axial plate' of Flower 1961). On either side of this is a layer of calcite fibres growing perpendicularly outwards, forming a non-septal stereozone. Quartz euhedra are common within these wall tissues in the Garra coralla.

Up to 44 septa have been counted, but the usual maximum for a corallum is 38–40. Normal adult corallites contain 32–36 septa (see text-fig. 16). The septa, of two orders, are thin in the tabularium, becoming gradually dilated outwards, until about 0.2-0.3 mm. from the periphery, where there is a rapid wedge-wise dilatation. These prominent septal bases merge with the fibrous wall tissue to form a narrow (*circa* 0.1 mm.) composite stereozone. The septal bases of adjacent corallites may be opposite or alternate. The major septa are unequal, and approach or interdigitate at the axis; generally one extends across the axis, or two opposite major septa may unite axially. The minor septa are



TEXT-FIG. 14. Xystriphyllum dunstani, SU 13263, $\times 6$. (a)–(e): transverse sections showing stages in the growth of a juvenile corallite. (f) longitudinal section through a single bud; (1) inception of bud, (2) appearance of first series of dissepiments, at a length of about 3 mm., (3) adult appearance attained, at a length of about 9 mm.

generally $\frac{2}{3}-\frac{3}{4}$ the length of the major, and extend some distance into the tabularium. The septa are commonly sinuous but never flanged.

 $Dt = circa \frac{1}{2}Dc$. The tabulae are crowded, complete and incomplete, moderately to deeply concave or often strongly funnel-shaped. Their margins are upturned.

There are 2–4 series of globose dissepiments, rather irregular in size. They are axially inclined, the inclination being moderate peripherally, increasing inwards. Those at the inner margin of the dissepimentarium are very steeply inclined or vertical and often elongate.

Ontogeny. Budding and the development of corallites has been reconstructed from the large number of sections made, although serial sections were not used (text-fig. 14).

Budding is peripheral. The bud forms in the corner of the parental calice with an initial diameter of about 1-1.5 mm. The first skeletal element seen in transverse section is a very short segment of wall tissue within the dissepimentarium (text-fig. 14*a*). The initial septa are inserted immediately in a very irregular pattern—the typical fourfold rugosan pattern apparently does not occur. The ends of the wall segment rapidly expand to meet the walls of the parent corallites, and septal insertion continues at a rapid rate (text-fig. 14*b*–*d*). At a diameter of about 2 mm. the first series of dissepiments appears; the corallite at this stage is about 3 mm. long (text-fig. 14*f*). Once the young corallite is completely enclosed by wall tissue it expands by a lengthening of all its wall segments, and so quickly assumes a polygonal shape, simulating an 'inter-mural offset' (text-fig. 14*e*). The second series of dissepiments appears about 4–5 mm. above the proximal extremity.

The above sequence suggests that in most, if not all, massive rugosan corals, the socalled 'inter-mural increase' (see Hill, p. F248, in Moore 1956) is in fact peripheral calical increase.

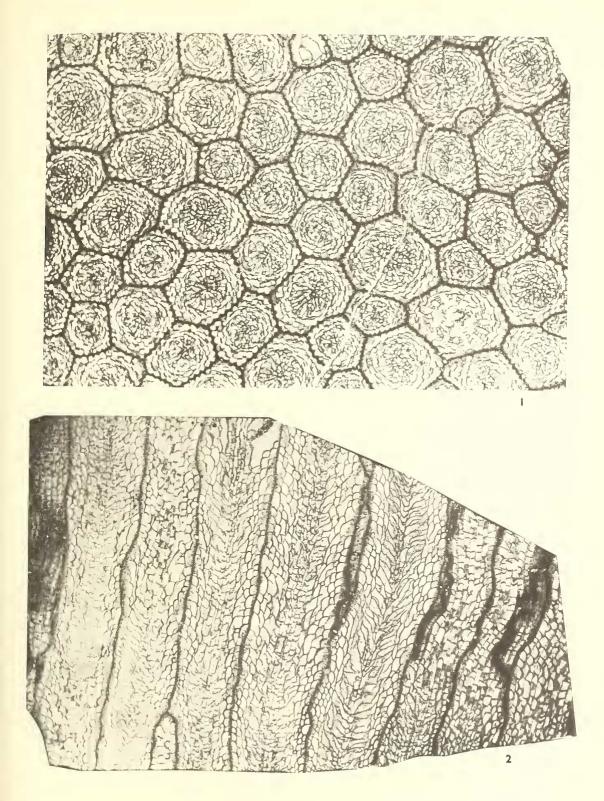
Variation (text-figs. 15–17). Dc, Dt, and n were measured for 6 coralla from the Garra Formation (up to 100 measurements of each), as well as 37 measurements of sections of 3 north Queensland coralla. It was found that frequency curves for all but Dc were of little value. Dc was plotted with a class interval of 0.7 mm.; the curves show considerable variation. Most are bimodal, with peaks at about 3–4 mm. and 5–7 mm. SU 5282 (loc. MM–12) and 13263 (loc. Cr–100) have skewed unimodal curves.

Bivariate plots of n:Dc for three coralla from loc. P-22 showed no significant differences, but that for the Queensland coralla was inconclusive (clearly about 100 measurements are needed from one corallum for great accuracy). In both this set of curves, and that for n/Dc:Dc, scatter diagrams show a marked change of slope in the region of Dc = 3.5 mm., and n = 28. This is interpreted as indicating rapid septal insertion in juvenile polyps, followed by slow insertion after the attainment of maturity, at an average diameter of 3.5 mm.

Comparison. As noted by Hill (1939b), *X. dunstani* is very similar to *X. mitchelli* (Etheridge fil. 1892). The latter has proportionately more septa, which show less tendency to inter-

EXPLANATION OF PLATE 92

Xystriphyllum dunstani (Etheridge fil. 1911). Transverse and longitudinal sections, SU 13263, loc. Cr-100; ×4.

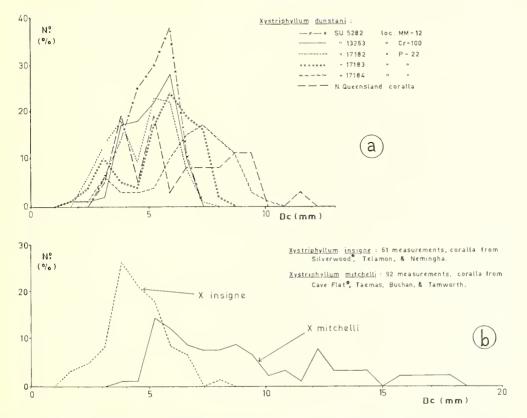


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digitate axially. Also, coralla of X. *mitchelli* from the Murrumbidgee Devonian may have much larger corallites (up to Dc = 18 mm.). Plots of n:Dc and n/Dc:Dc show significant differences from those for X. *dunstani* (text-figs. 16, 17). The plot for n/Dc:Dc has the same form as that for X. *dunstani*—perhaps, therefore, a generic character—but differs in that the change of slope occurs at $Dc = circa \ 6 \text{ mm.}$ A further morphological

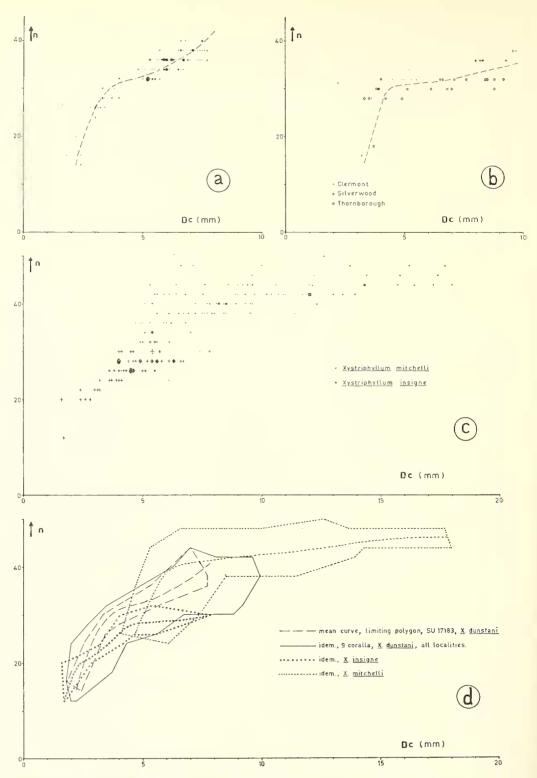


TEXT-FIG. 15. *Xystriphyllum spp*. Frequency polygons for Dc. (*a*) five Garra coralla and coralla from north Queensland localities (combined), *X. dunstani*; (*b*) coralla of *X. insigne* and *X. mitchelli*, including * type localities.

distinction between the two species is in the nature of the peripheral septal dilatation. In *X. dunstani* this is wedgewise and distinctly triangular in transverse section. In *X. mitchelli* the dilated portions are longer and often ogival in section.

Scatter diagrams for X. insigne Hill 1940 are much closer to those for X. dunstani than are those of X. nutchelli (text-figs. 15–17), but the two species are readily distinguishable morphologically. X. insigne is smaller than X. dunstani, with fewer septa and proportionately thick walls.

Remarks. Stenophyllum gorskii Bulvanker in Krayevskaya 1955, from the Coblenzian and Eifelian of Asian U.S.S.R., cannot be distinguished from the type sections of *X. dunstani*. Despite the considerable geographic separation, I at least tentatively place



TEXT-FIG. 16. Xystriphyllum spp. Variation of n:Dc. (a) scatter diagram for X. dunstani, SU 17183 (Garra Formation) with mean curve obtained from density-contouring of plot; (b) idem, north Queensland X. dunstani; (c) scatter diagrams, X. insigne and X. mitchelli; (d) comparison of mean curves and limiting polygons for the three species.